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POLLUTION EFFECTS ON THE FUNGUS POPULATION OF A STREAM

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It has been assumed generally that fungi form an insignificant part of the biota of streams and other bodies of water. Occasionally results of work appear showing that fungal members of a population have been sampled, but no attempt is made to quantitate such studies. This situation has resulted partly from sampling technique limitations, and partly because most investigators of aquatic fungi are primarily interested in morphological, taxonomical, physiological and genetical aspects of peculiar or unusual types, rather than in assigning such fungi a role of special importance as members of a population.

In general, fungi have not been considered nuisance organisms in streams. The activities of the "sewage fungus" *Sphaerotilus*, a bacterium, far outshadow in the minds of aquatic biologists, those ascribed to true fungi. The techniques of the students of bacteria, plankton and benthos appear to be better known to the students of stream sanitation. Since these techniques do not lead to the ready definition of a mycobiota of any body of water, it is not convenient to investigate such a mycobiota.

For those studying true aquatic fungi, novelties and algal parasites though they be, should any other type of fungus develop in a culture it is almost automatically a contaminant, not necessarily a member of a specific population which may have developed in the habitat being sampled (but see Sparrow 1935). However, when the techniques of the soils mycologist are applied to various types of stream or stream-bed samples, a large population of geofungi can be found. Before describing the populations observed in Lytle Creek, Clinton County, Ohio, it may be pertinent to review the state of aquatic mycology, to discuss the potential role of geofungi in aquatic environments, and appraise critically fungus culture techniques.

HISTORICAL OBSERVATIONS

In reading Klein (1957) and Edmondson's revision of Ward and Whipple's *Fresh Water Biology* (1959), I concluded that the students of aquatic biology in general have overlooked a considerable field by neglecting certain aspects of fresh-water mycology. In Edmondson (1959), Sparrow said: "The bulk of the true fungi occurring in fresh water belong to the Phycomycetes although there are a few aquatic Ascomycetes and Fungi Imperfecti." The writer would like to paraphrase the first half of this sentence to read: "The bulk of the true fungi occurring in fresh water and observable directly or by culture on special baits, belong——." This statement more nearly corresponds to actual practice, for most observers of fresh-water fungi do not use plate culture techniques for their studies. In spite of this defect, a wealth of fungi can be observed in fresh-water studies, for Sparrow keys out 104 genera of Phycomycetes and 6 of Ascomycetes, while Scott, in the same chapter, presents a key to 21 genera of fresh-water aquatic Hyphomycetes whose spores are readily observed and identified by microscopic examination. Neither Sparrow, Scott, nor Edmondson indicate that other kinds of fungi may be found in the habitats considered in the book. Since in this volume, Stanier and other writers include species which may be associated with pollution of one sort or another, the following review and discussion will include organisms usually assigned to the fungi which may be found in clean or polluted fresh water.

Odum (1953) states in his ecology text: "While bacteria and fungi may be beyond reach at first, their importance should not be forgotten." Except for the mycologists who studied the aquatic fungi, whether Phycomycetes or Hyphomycetes, few persons working with the biota of clean or polluted fresh waters have considered

the fungi important, partly because the techniques of search for these fungi are mostly restricted to the laboratory of the specializing mycologist, partly because vegetative and reproductive structures and organs are not as readily observable as are algal and protozoan cells, and partly because no important mycological disease of plants, animals or man has been referred to fresh water habitats.

Because of his wide experience in mycology, Weston (1941) was able to say:

Of the fungi, only one group is predominantly aquatic, wholly adjusted to a completely submerged life, and giving every indication of being aquatic both in origin and in subsequent evolution. That group is the aquatic series of the Phycomycetes. To be sure, some representatives of other groups are adventives in aquatic habitats; . . . and a few genera . . . may perhaps be even more definitely adapted to aquatic life. Such are the water fungi, a group ubiquitous, abundant, versatile, hardy, and efficient, playing a significant part in the complexly interwoven pattern of biologic interaction in inland waters; as saprophytes in manifold capacities unceasingly active in the essential degradation of complex materials; and as parasites ever preying inconspicuously on the major groups of plants and animals important in hydrobiology, and occasionally so severely destructive as to reduce productivity.

Weston's students did not demonstrate their teacher's confidence in the water molds quantitatively, but the wealth of work they and their students have produced is testimony to the varied populations involved. In addition, the adventives and the reinaders are of considerable importance, and the parasites are truly destructive.

In a chapter in Phelps (1944), Lackey made some pertinent remarks about the quantitation of the microbiota and its role in the biota of the stream:

But for the microscopic inhabitants of lotic environments, information is decidedly scant. This applies particularly to the fungi, algae, protozoa, . . . Each of these groups is common at some time to some stream stretch. Their numbers indicate a successful adaptation to one of the most changing of all environments, flowing water. Bottom dwellers are especially important in the decomposition of organic matter.

In the text by Ruttner, translated by Frey and Fry (1953), there are several statements pertinent to the potential role of fungi in stream biology: "The multitude of fungi is represented (in the plankton) only by a very few primitive species, which are seldom encountered, a circumstance attributable less to the shape than to the mode of life of these organisms." The methods of observation and collection of these organisms are additional blocks to their successful quantitation and the proper evaluation of their role in the life of the stream. "The *Aufwuchs* on suitable substrates does not stop by any means at the lower limit of a positive assimilation balance, the depth of which naturally is dependent mainly on the transparency of the particular lake. However, here in the profundal it does not consist of assimilating algae, but rather of heterotrophic organisms—primarily sessile animals and less frequently fungi growing on wood"; and, concerning populations of the bottom ooze,

It should be strongly emphasized that these are only a few examples of the endless variety of bacterial processes, still much too little understood, which take place in water; that in addition there participate in these processes not only bacteria but also aquatic fungi (for example, the Saprolegniaceae), algae, flagellates, ciliates, and the higher animals of the ooze biocoenosis, which nourish themselves on these organic materials, partly assimilating them and partly excreting them as simpler compounds.

Other pertinent information, with an emphasis on sanitary engineering more than ecology will be found in an earlier review (Cooke 1954a).

Three principal groups of fungi have been studied by mycologists in the delineation of the mycobiota of streams, lakes and other bodies of fresh water. Two of these, the parasites of plankton and other aquatic organisms and the saprobic aquatic fungi, are classed with the Phycomycetes, the third includes certain genera of specialized Hyphomycetes in the Fungi Imperfecti. Basidiomycetes have been found only recently in aquatic habitats (Ingold 1959) and are represented only by aquatic Hyphomycete-like species with clamp connections at the septae. While the aquatic Phycomycetes possess flagellated spores which enable them to swim, Ingold (1953) speaks of the value of the zoospore to the parent organism: "It is interesting to consider the biological value of the zoospore as contrasted with a non-motile spore. So far as actual transport is concerned, the motility of the zoospore has little

advantage over the non-motile spore, since the actual movement of water in a pond, lake, or stream is probably great in comparison with the feeble efforts of a zoid. The value of the zoospore would seem to reside in its power to 'select' the substratum on which it settles by virtue of its taxisms." He implies that species of fungi with nonmotile spores require a larger number of spores in order to overcome the accidents of chance in the settling of spores upon suitable substrata.

The true aquatic fungi, those having motile spores or sex cells or both, have been known for a long time. The first species in the filamentous group, the Saprolegniales, was described as early as 1821 (Coker 1923), and in the holocarpic group, the chytrids, in 1844 (Karling 1942). Probably because the student of these fungi uses specialized techniques, their study has been restricted to a few laboratories where workers have been more assiduous than usual in the search for them. From such laboratories has come a wealth of literature describing species in detail, and habitat and occurrence in general. This work has been summarized in several principal monographs.

It is as true today as it was in 1923 (Coker) that: "Aside from the dates and places of collection given incidentally and usually in meager numbers by systematic writers, little is known of the occurrence, periodicity and environmental factors involved in the growth of the Saprolegniaceae." Even the presentation of a percentage-occurrence table for water molds isolated from 593 water samples, collected between Feb. 15, 1912 and Dec. 12, 1913, from all sources within and around Chapel Hill, North Carolina, was not sufficient stimulus to later students to develop a quantitative technique for understanding or presenting this type of population. Karling (1942) and Sparrow (1943), in monographic treatments of holocarpic and other nonsaprolegniaceous members of the aquatic fungal population, presented habitat and distribution data as well as methods of collection, but neither author suggested methods of obtaining quantitative descriptions of populations.

For a year Harvey (1952) isolated aquatic fungi from clean to polluted fresh-water streams in Southwestern Ohio, principally in the Little Miami River basin. Among his conclusions, he stated: "When water carries even a small amount of organic matter, fungal activity should be anticipated. Although very few fungi have been seen actually living in water, their spores may be obtained therefrom plentifully." In Harvey's study no attempt was made to develop a technique for

the quantitative demonstration of water molds, nor did Cooke and Bartsch (1959, 1960) reach a point beyond which the development of a quantitative technique would be helpful in demonstrating the presence of a biota of aquatic fungi indicative of degrees of pollution.

In 1954, Höhnk and Bock reported on their efforts to describe the aquatic fungus populations of lakes in Germany. They were able to demonstrate the occurrence of different species at several levels within one body of water.

In his monograph on the genus *Achlya*, Johnson (1956) described the methods for demonstrating the occurrence of fungi of this genus. His only citation of quantitative techniques was his study of frequency distribution. Some investigators may infer from the description of baiting techniques that one colony of mold on any type of bait represents the results of the activity of one spore of a homothallic species, or at least of two spores of a heterothallic species. The area on a hemp seed available for colonization is so great, compared to the size of potentially colonizing spores, that a colony may be produced by several spores and even by spores of several species.

Canter (1950, 1951, 1954) and Canter and Lund (1948, 1951, 1953) have described the occurrence of various chytridiaceous algal parasites at various seasons of the year. The best means of quantitation of this segment of the population appears to be expression of its effects on the algal biota.

Parasitism of one alga may favour the development of other algae. Other things being equal at the time of the maximum, dominance of species with similar demands on the environment will depend on the relative size of the populations at the start of the periods of increase. The observed degree of infection of the algal population depends on the relative growth rates of host and parasite. However, if conditions are suitable, the parasite can grow faster than [the alga] can at any time in the lakes concerned. This is shown to be the case by the fact that epidemics may occur at any time of the year and be preceded or followed by rapid growth of [the alga]. Occasionally the occurrence of an epidemic may coincide more or less closely with the period when the host population is about to decline from other causes (Canter 1954).

Recently, several workers have become interested in the aquatic Hyphomycetes, those mold-like fungi which produce spores apparently readily adapted to dispersal in water. C. T. Ingold (1953,

1954) has been interested in this group of fungi in England and has contributed much in recent years to our knowledge of the group. Concerning their habitat, Ingold (1953) says:

One striking and abundant flora of aquatic Hyphomycetes is regularly to be found on submerged, decaying leaves of deciduous trees and shrubs in well-aerated water, particularly in small streams that are not too sluggish. They occur especially on the petioles and larger veins, the branched septate mycelium ramifying in the decaying leaf tissue and the conidiophores projecting at right angles into the water. The whole story of dispersal is strictly aquatic, the spores being produced, liberated, and dispersed below water.

In describing the method of collecting spores of these fungi, Ingold (1954) says:

Some attention has been directed in recent years to the 'spora' of the air, but there is a spora of the water too. In a babbling brook a brown foamy scum often collects behind a barrier of twigs. If this is collected and examined under the microscope, especially in autumn and winter, a wonderful collection of spores can be seen with tetra-radiate ones predominating. If such a preparation is compared with the aerial catch by slit samplers the amazing differences between the spora of the air and of the water of a stream are at once apparent.

On the other hand, Ranzoni in California (1953) found these fungi in a different modification of the aquatic habitat. In parts of California are ephemeral streams, ponds and other bodies of water.

When skeletonized leaves were collected, either from stream beds or ponds several months after the water had evaporated or from debris left behind by the floods, and placed in water, it was found that sporophores and spores were formed in large numbers after about 48 hours. What the "holding-over" mechanisms are here is not yet known. It is assumed for want of other evidence that it is the thicker-walled, more densely pigmented hyphae, such as are formed in culture, that act to hold the organism over until favorable conditions return.

Both Ingold (1954) and Ranzoni (1953) attempt to explain the benefits to the fungus of the

development of a means of dispersal such as the tetra-radiate spore. According to Ingold:

Since the tetra-radiate spore has so clearly been developed over and over again in these Hyphomycetes it is reasonable to suggest that it may have some biological significance in the aquatic environment. Perhaps such a spore sinks more slowly and so stands a better chance of dispersal, but it seems to me more likely that its importance lies in it being a minute anchor which may easily become entangled in a suitable substratum. In a stream the coming to rest of the spore in a position suitable for germination may be a real problem.

And Ranzoni makes a further observation:

... one of the more important features of the branched and sigmoid form of (the spores of) the aquatic Hyphomycetes is the resistance that these shapes offers to the movement of water. As observed in water cultures, these spores float very efficiently and are doubtless carried long distances by the movement of water in the natural habitat.

In Europe, Glen-Bott (1951) and van Beverwijk (1951) have reported on several unusual "aero-aquatic" fungi identified from spore masses on leaves recovered from the bottoms of apparently stagnant lakes.

Throughout this discussion of the general biota of streams and of the special biotas of aquatic fungi, it has been stated or hinted that certain more prosaic types of fungi also occur in the habitat. These are the fungi with which the bulk of this report is concerned. They are without special organs of dissemination capable of searching out a special food supply, without special organs on the spores to aid in anchoring the disseminule or to resist the movement of water. These fungi reproduce, but poorly, by means of spores in an aquatic environment. If a piece of mycelium would come to the attention of the plankton or benthos specialist microscopically studying incidental samples, the type of spore-producing structures would be so atypical, as a result of having been produced in water, that the available keys, should they be used, would provide little assistance. If the spores of these fungi become embedded in accumulated foams, as described by Ingold, they would be readily overlooked, usually on the basis of size and recognizability. If colonies of these fungi develop in the same cultures in which chytrids or saprolegniaceous fungi are being studied, they

would be discarded as contaminants, for the spores of many of these species are common in the air, especially of laboratories and other closed places.

Lackey, in Phelps (1944), discussing the populations of organisms at the source of a stream, in this instance a spring, stated: "Bacteria and fungi were not counted but were present. (It is clearly shown): 1. water immediately emerging from the ground contains enough plant food to support a large population; 2. this is immediately browsed upon by animals, and a mixed population is established; 3. aged water is not necessary for a bottom-dwelling population." If this is true for the source of a stream, how much more is it true of a stream several miles from its source, especially after receiving runoff from barnyards, septic tanks, woodlands, fields, and other habitats in which plant and animal wastes are a normal part of the load no matter how dilute they may be in the water.

A check-list of the fungi found in polluted water and sewage, obtained by using techniques of the soils scientist (Cooke 1957), as well as a brief description of the mycobiota of Lytle Creek have been published (Cooke 1954c).

BIOLOGY OF GEOFUNGI

On a habitat basis, we may consider the fungi which have been mentioned as belonging to two principal groups: 1. The *hydrofungi*, those species whose life cycle is adjusted to be completed in water, including water present only as a film sufficiently thick to permit the swimming of the zoospores or gametes. These, then, include the aquatic Phycomycetes of both the holocarpic and filamentous types, and the aquatic Hyphomycetes whose special branched or sigmoid spores are always produced under or on the surface of water. 2. The *geofungi*, those species familiarly known as the soil fungi, which are not especially adapted to an aquatic existence but whose life cycle may be completed under water because of an adequate supply of nutrients. The first group includes obligate aquatic fungi; the second includes facultative aquatic fungi.

According to Garrett (1956), the life cycle of a saprobic fungus living in the soil is as follows: a piece of dead organic matter such as a root, piece of leaf or stem, etc., comes to rest near a spore of a fungus. Activated in some way by the presence of this nutrient, the fungus spore germinates, the mycelium uses that fraction of the dead organic matter available to it, goes into a resting condition by producing a large number of spores, and the cycle is complete. In any body of water two types of nutrient materials are available to the fungi. The first is in the form of solid organic

matter in suspension or settling out onto the bottom. Here, if such a fragment and a spore capable of using it are brought together, the cycle described above will become operative. However, dissolved in the water are other nutrients some of which will be readily available to the fungus. Upon germination of the spore, the fungus proceeds to grow indefinitely in the presence of this continual bath of nutrient materials no matter how dilute. Depending on the supply of nutrients and the ability of the fungus to grow indefinitely, a small to large mass of mycelium develops. Occasionally this mycelium may sporulate, but such spore production is atypical. In periods of flood, scouring action of inert materials in the stream bed results in the removal of much, if not all, of this growth. That not completely removed may continue to produce a new mycelial mat, that washed away may come to rest as a single mass or as many small fragments in other parts of the stream bed or on the bank above the influence of the water. Depending on its ability to adjust to the new conditions of existence, the mycelium may die, may go into a resting stage, or may continue to live, growing at the expense of dissolved or solid suspended organic matter in the water. Depending on such stream conditions as available nutrients, ability of existing spores to germinate and of existing mycelium to continue growth, the fungus population will be small to large, yet the techniques of the plankton or benthos student will not demonstrate the presence of such growth to any extent. Fragmentation of mycelium, mixtures of algal and fungal growths in slimes on stones or other substrata, and techniques of sample collection tend to disguise the nature of the total sample and the observer tends to ignore the presence of this segment of the population. In addition, the average observer of plankton and benthos samples, untrained in esoteric aquatic mycology, will have little or no basis for recognizing a fungus under his microscope.

In the preliminary stages of developing techniques for sampling aquatic habitats for fungi, it became apparent to the writer that the geofungi might play some role in the breakdown of organic materials in waters of many kinds. With this idea in mind, sampling was undertaken using the techniques of the soil scientist. The development of these techniques has been described in earlier contributions (Cooke 1954b).

IMPLICATIONS OF DIRECT AND PLATE COUNTS WITH RESPECT TO FUNGI

Fungi and bacteria are among the more difficult organisms with which to work, on the basis

of direct counts, when the observer is considering a plankton or benthos population. Both types of organisms are colorless and most of the cells, in the preparations under observation by the counter, are of such a size and resolution that they escape attention. In a bacterial bloom, such as that produced by *Sphaerotilus natans*, less difficulty is encountered because the bacterial cells are arranged in chains enclosed in or bundled up in filaments of a slime-like substance. Colonies of the bacterium *Zoogloea ramigera* are also relatively easily observed when they occur in sizes indicative of unusual fertilization by stream additives. Spores of the common aquatic Hyphomycetes and of a few of the genera of hyphomycetous soil fungi found in streams are also fairly readily observed.

The population of fungi in an aquatic environment is largely thought to consist of algal parasites, easily baitable chytrids and saprolegniaceous fungi, and aquatic Hyphomycetes with elaborate and highly specialized spores. So far, no one has presented an adequate method of quantitating the occurrence of such fungi and one can only guess at the role of these fungi in the purification of even naturally polluted waters.

Plating techniques (Cooke 1954 b, c) for the study of other types of fungi in streams yield a different type of information. The original sample of the material to be tested for fungi is shaken in a volume of water to separate the spores from the parent cells and to break up longer pieces of mycelium. When the fraction to be tested is plated, it includes only a small portion of the original material, ideally only enough to develop a maximum of 40-60 colonies per plate. What do these colonies represent and how can they be interpreted quantitatively in respect to the total mycotic population in the sampled habitat?

A fungus which is a normal member of the population of organisms in an environment of any kind, unless it is one-celled or is composed of a pseudomycelium as in the yeast and the so-called filamentous yeasts but not in the false yeasts, is composed of many hyphae which form the mycelium from which sporophores are produced on or in which spores are borne. The sporophore may be simply a hypha which breaks up into many arthrospores, or it may be a more elaborate, or even a highly specialized, structure. The hyphae of the mycelium are usually attached to some object. This object may be fixed to the bottom of the stream, in which case the fungus becomes part of the benthos. It may be attached to a fragment, macro- or microscopic in size, of material containing substances which act as nu-

trients for the fungus, in which case the growing organism is part of the plankton. If zoospores are swimming, or nonmotile spores are floating, on the surface of a pond or in the current of the stream, they may be considered a part of the stream or of the water spora which is part of the plankton. Within a natural habitat such as a soil a fungus will continue to grow in its assimilative phase until its food supply is exhausted, when it will produce its spores and go into a resting period. However, under conditions in which the fungus is submerged, the production of spores by the adventive population of geofungi appears to be accomplished in ways atypical of growth in an aerial habitat. The sporophores, when present, are reduced in size and number, and the spores are produced in smaller numbers. This may result from the habitat in which nutrients are less abundant, and spore production conditions are different, or from other factors. Where nutrients are continually added from stream source to mouth, the fungus population is continually bathed in a nutrient solution so that spore production may not be a necessary factor in the existence of the fungus. Thus in an aquatic environment the fungi may be present primarily in the assimilative phase.

Spores are present in any environment as single complete structures. The mycelium is an accumulation of a series of elongate tubes sometimes divided into cell-like structures, sometimes not. In breaking up a mycelium on the shaker to determine something of the number of disseminules present, each cell, if separated from the other cells of a mycelium, could become a disseminule capable of disseminating and reproducing the parent organism. It would be necessary to break the mycelium at each alternate cell in order to obtain a completely accurate idea of the number of disseminules the mycelium was capable of producing. Obviously, this is impractical if not impossible. Thus any statement concerning the quantity of fungus colonies present in any habitat is subject to error. To date, no way has been discovered to overcome this type of error so that a fungus producing a large crop of spores is usually thought to be more abundant than a fungus capable of producing few spores but able to perform large amounts of "work."

The counting of a bacterial or a yeast population, on the other hand, is merely reporting something concerning the numbers of bacterial or yeast cells present in an environment at the time of sampling and, except for the species whose cells are "glued" together by means of mucilaginous envelopes, can present a fair representation

of the type of population developed on any of the several types of selective media chosen for the survey.

Before considering the techniques for the study of the geofungi of Lytle Creek and the population found in that stream, a survey of the information available on the geography of the area and of the physical, chemical and biological factors of the stream will be presented as a description of the characteristics of the habitat of the mycobiota encountered.

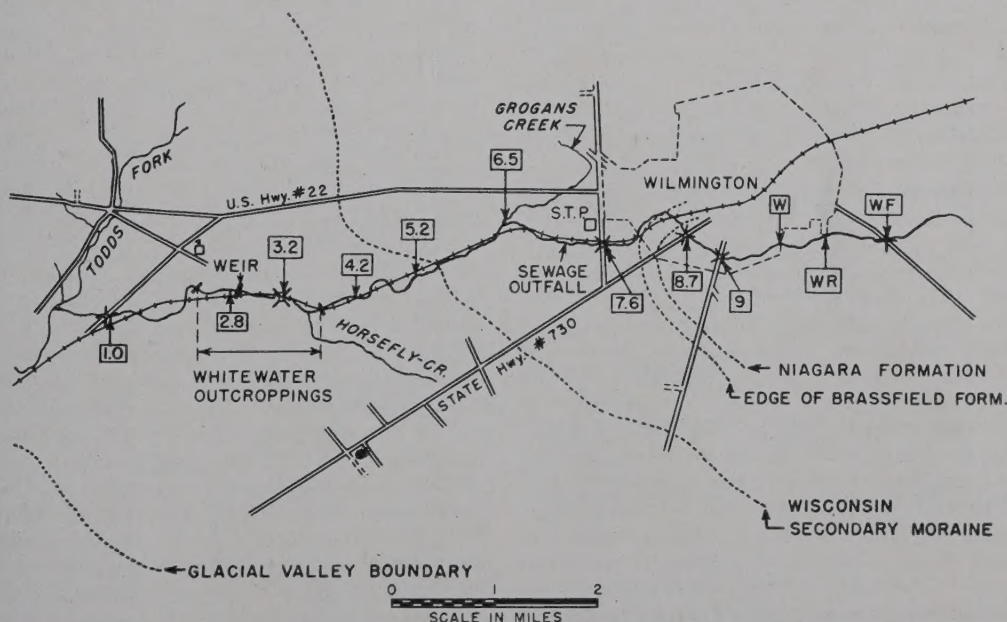
LYTLE CREEK

Geography

Lytle Creek (Paine and Gauvin 1956) lies in the Little Miami River Basin. It flows into Todd's Fork, a tributary of the Little Miami river. Its mouth is about 45 miles northeast of Cincinnati. It drains about 27 sq miles of land of which about a third lies in the City of Wilmington, a community of 7,412 people, according to the 1950 census. Although Lytle Creek is considered a permanent stream, the sewage effluent from the Wilmington sewage treatment plant comprises 80-100% of the stream flow during low flow stage in summer and autumn. The creek is approximately 11 miles long and has an average gradient of 20 ft per mile, according to the Blanchester Quadrangle U.S.G.S. Map

(1931). It is 3-35 ft wide during low water stages and varies in depth from a few inches in the riffles to more than 6 ft in at least two pools.

East and north of the city its flow is weak, being strengthened by minor tributaries, outfalls and seepages from septic tanks and other run-off from farms in the region. Through the city it receives outfall from individual sanitary drains not tapped into the Wilmington sewage system, as well as street drainage and storm run-off. Just outside the western city limits it receives the outfall from the Wilmington sewage treatment plant. At various times the stream has received raw sewage, first because of a break in the trunk sewer about a half mile above the plant and second because effluents from a dairy and a metal shop drain directly into the creek. At the time of samplings reported here, the sewage treatment plant was a primary type with chemical precipitation and the run-off in the outfall was rich in organic materials. An average of approximately $\frac{3}{4}$ million gallons of sewage were treated daily. The sewage was of the combined type and during periods of heavy rain a large part of the total flow was bypassed directly into the creek. This resulted in a pool at the outfall whose bottom was highly septic. In the summer of 1954 the treatment process was changed to activated sludge which resulted in a marked change in the nature



LYTLE CREEK DRAINAGE BASIN

Figure 1.

of the stream as mentioned briefly in an earlier report (Cooke and Bartsch 1959).

At the outfall from the sewage treatment plant a turbid condition occurred, although water generally appeared relatively clear. However, the growth on the stream bed and banks and the resulting odors indicated that during the first mile, or at some seasons 2 miles below the outfall the turbidity supported a population of organisms related more to pollution than to clean water.

The stations on the creek (Fig. 1) are numbered according to their measured mileage from the mouth at Todd's Fork. They were chosen during the early phase of the study for their access to roads as well as for their apparent abilities to demonstrate the typical biotic characteristics of the major pollution zones; thus they are not equidistant.

The major habitat conditions as of July 10, 1952, are recorded in Table I. They are not necessarily those of the present time, as the creek bed at some places has been arbitrarily altered. Certain stream bed characteristics also have changed in the last five years as a result of the changeover in sewage treatment which has resulted in a different type of effluent and aquatic environment.

TABLE I. Habitat conditions, July 10, 1952, Lytle Creek

Station	Bed	Bottom	Bank	Border
1.0	Gravelly	Clean	Coarse sandy	Willow shrub
2.8	Flat native rock		Rock ledges	Grassy meadow with marshy springs
4.2	Gravelly	Clean	Muddy to sandy	Tree lined
5.2	Gravelly	Masses of attached <i>Sphaerotilus</i>	Sandy to gravelly	Meadow with occasional sycamores
6.5	Gravelly	As 5.2 but with occasional blanket of <i>Sphaerotilus</i>	Sandy	Open meadow
7.2	Sandy-gravelly	Septic sludge	Muddy to sandy with septic organic matter	Tree and shrub lined; sewage treatment plant outfall
7.6	Sandy-gravelly	Clean, green algae in pool	Sandy-gravelly	Tree lined, one bank formed from city dump refuse
8.7	Gravelly	Clean	Sandy-gravelly	Willows and meadow, open

Physical-Chemical Conditions

The temperatures (Table II) of the sampled habitats were taken at the September, 1952, January, February, and March, 1953, sampling

periods. They were taken with a stab thermometer registering degrees Centigrade, placed at the sampling points and allowed to come to equilibrium with the habitat before being read. At each of the 8 stations, 4 types of samplings were taken by scooping materials to be tested into metal soil cans: 1. water from the stream, 2. water and sediment in a pool, 3. water and sediment in a riffle, and 4. bank soil which was always wet and always subject to extra irrigation during periods of high water. At the laboratory these samples were diluted once, twice or three times depending on numbers of mold colonies expected from each, as determined by platings made from the first set of samples taken in March, 1952. From a 1:10 dilution the supernatant was withdrawn and the pH was taken using a glass electrode pH meter (Table III).

TABLE II. Temperatures of Lytle Creek habitats (in degrees C)

Stations	DATES			
	9-18-52	1-14-53	2-25-53	3-30-53
Water				
8.7	18.0	4.5	3.0	8.0
7.6	18.0	4.5	3.0	8.0
Effluent	7.2	9.0	7.5	11.0
6.5	21.5	6.0	5.0	9.5
5.2	19.0	6.5	5.0	9.5
4.2	19.0	5.0	4.0	8.5
2.8	18.5	4.5	3.5	7.5
1.0	18.5	4.0	2.5	8.0
	18.5	3.5	2.5	8.0
Water and sediment in pool				
8.7	18.0	5.5	3.0	7.0
7.6	18.0	5.0	3.5	7.0
7.2		7.0	4.0	11.5
6.5	19.5	7.0	4.5	8.5
5.2	19.0	5.5	4.0	8.0
4.2	18.5	4.5	4.0	7.0
2.8	18.5	4.0	3.5	8.5
1.0	18.5	8.0	6.0	9.0
Water and sediment in riffles				
8.7	18.0	5.0	2.5	7.5
7.6	18.0	4.5	3.0	7.0
7.2		6.0	5.0	9.0
6.5	19.0	6.0	4.5	9.0
5.2	18.5	5.0	3.0	7.0
4.2	18.0	4.5	3.0	7.0
2.8	18.0	4.5	2.0	8.0
1.0	18.0	4.0	3.0	6.0
Bank soil				
8.7	18.0	6.0	1.5	8.0
7.6	18.0	5.0	1.5	8.0
7.2		5.0	3.0	16.5
6.5	18.0	5.5	3.5	9.0
5.2	18.0	5.0	1.0	7.0
4.2	17.5	4.5	0.5	9.0
2.8	17.5	4.5	1.0	12.0
1.0	17.0	5.0	2.0	8.5

Air temperature: 20-25

10.0-11.5

TABLE III. pH Levels of Lytle Creek habitats

Stations	DATES			
	9-18-52	1-14-53	2-25-53	3-30-53
Water				
8.7	7.8	7.1	8.2	7.2
7.6	7.6	7.4	8.1	7.9
Effluent		7.3	8.0	7.6
7.2	7.4	7.3	8.1	7.8
6.5	7.6	7.2	8.0	7.8
5.2	7.8	7.3	8.4	7.8
4.2	7.9	7.2	8.2	8.0
2.8	7.8	7.4	8.1	8.2
1.0	7.8	6.6	8.2	8.0
Water and sediment in pool				
8.7	7.9	7.8	7.3	7.2
7.6	7.6	7.8	7.0	6.9
7.2		7.4	7.2	7.1
6.5	7.1	7.3	6.8	7.0
5.2	7.5	7.5	7.4	8.0
4.2	7.6	7.5	7.2	7.2
2.8	7.4	7.6	7.8	7.2
1.0	7.5	7.7	7.5	7.2
Water and sediment in riffles				
8.7	7.8	7.8	7.9	7.8
7.6	7.5	7.9	7.4	7.7
7.2		7.4	6.7	6.6
6.5	8.2	7.8	7.7	7.5
5.2	7.5	7.3	8.5	7.6
4.2	7.5	7.2	7.8	8.2
2.8	7.4	7.5	7.5	7.1
1.0	7.8	7.7	7.8	7.6
Bank soil				
8.7	7.6	7.8	7.7	7.3
7.6	7.6	8.2	7.5	6.4
7.2		7.8	7.3	8.3
6.5	7.9	7.1	8.3	7.7
5.2	7.6	7.6	7.6	7.4
4.2	8.0	7.8	8.5	8.2
2.8	7.9	7.7	8.3	7.0
1.0	8.2	7.5	7.4	8.2

Data in Table IV were accumulated from the records of the U. S. Weather Bureau and were converted to degrees Centigrade and millimeters of precipitation. In addition to maximum and minimum temperatures recorded at Wilmington for the dates on which samples were taken along Lytle Creek, this table presents the average maximum and minimum temperatures for each month during the period of sampling. Precipitation data also are included. Without the sewage treatment plant effluent, the character of Lytle Creek would be one of intermittent flow and varying levels. During the sampling period this intermittent character was expressed more in flood conditions carrying excess runoff from heavy precipitation.

The temperature records clearly indicate that the temperature of the water in Lytle Creek is directly influenced by the temperature of the discharge from the sewage treatment plant regardless of the season. The water temperature is al-

TABLE IV. Temperature and precipitation data, Wilmington, Ohio

Date	TEMPERATURE °C				Precipitation (mm)
	Mo. Average		Actual		
	Minimum	Maximum	Minimum	Maximum	
March 27, 1952	-0.83	10 0	-1.67	7.22	115.57
April 17	4.22	17.11	0.00	18.89	113.28
May 15	9.94	22.33	15.56	25.00	107.19
June 12	16.72	30.67	12.78	23.89	109.98
July 10	17.06	31.94	8.32	27.22	32.77
Aug. 17	14.89	29.72	16.11	30.56	66.29
Sept. 18	10.22	26.33	13.89	24.44	64.52
Oct. 23	1.61	17.44	-0.56	20.00	31.24
Nov. 26	0.56	12.22	3.89	14.44	49.28
Dec.	-2.28	5.28	—	—	108.71
Jan. 14, 1953	-3.06	6.67	2.78	12.78	145.29
Feb. 25	-3.78	8.39	-3.33	5.56	36.32
Mar. 30	0.28	11.78	-4.44	9.44	67.56

ways warmer than the minimum air temperature and cooler than the maximum. For at least two miles below the Wilmington outfall, the temperature of the stream bottom in pools and riffles was also affected by the temperature of the sewage during the period in which temperatures were taken, except in February when the effect was noted for only a mile. Temperatures of the bank soil were so variable during the late winter and early spring that no correlation can be made between effect of sewage temperature and temperature of the creek water. Other factors of the habitat which have not been considered in this study are probably operative here.

Biology

Many phases of the biology of Lytle Creek have been reported in the literature, largely in reference to planktonic, insect, and fish life. In these reports can be found additional data concerning the chemical and physical conditions of the stream throughout the year or at stated times. Confirming such earlier work as that of Weston and Turner (1917), Gaufin and Tarzwell (1952, 1956) in summarizing work on macroinvertebrates and vertebrates found that the quantitative and qualitative composition of an aquatic population constitutes a valuable index of the zones of pollution in a stream, that all environmental factors should be considered in evaluating populations of a stream, that pollution associations are characterized by few species but large numbers of individuals, and that pollution-associated organisms must be adapted to periods of low or absent oxygen supplies.

Harvey (1952) listed 8 species of aquatic Phycmycetes from Lytle Creek samples obtained in routine samplings and in one 24-hour run of the

stream. He found no species in the septic zone at the point of outfall of the sewage treatment plant. Best representation of these fungi was found in the clean water zones above the source of pollution, in the clean water in the lower reaches of the creek, and in the upper part of the zone of recovery below the outfall. In checking the Creek after the changeover from primary treatment of sewage to secondary treatment with activated sludge, Cooke and Bartsch (1959) found considerable uniformity among aquatic fungus populations at all stations. Cooke (1954c) found little correlation between the numbers of species of soil fungi present at any one time or place and the number of colonies produced in plating the samples. Cooke has presented a combined list of the fungi (1957) and yeasts (Cooke *et al.* 1960) found in polluted waters and sewages. These lists include a number of entries from Lytle Creek records.

In 1950, samples of Lytle Creek water showed that, in March, just below station 7.2, only 50% of the flow was represented by sewage, while in August, 94% of the flow was attributable to sewage. In March, comparative checks of stations near the outfall showed that 99.59% of the coliforms were contributed by the sewage influent while in August this value was 99.95%.

Phytoplankton in the water within two miles of the sewage outfall in July, 1950, were listed in unpublished data by Dr. C. M. Palmer. These data, presented in Table V, are averages based on 6 sets of samples taken at 2-hour intervals in one 24-hour period. Data for the principal genus in each category are presented beneath those for the category.

TABLE V. Phytoplankton organisms recorded as numbers per ml (average of 6 samples)

Type of organism	STATIONS			
	7.6	7.2	6.5	5.2
Total phytoplankton....	68	42	220	643
Diatoms.....	57	23	121	200
<i>Nitzschia</i>	37	21	118	190
Green-algae.....	2	1.5	5	21
Blue-green Algae.....	5	7	23	119
<i>Oscillatoria</i>	2	6	14	101
Pigmented flagellates...	4	10	71	303
<i>Euglena</i>	1	7	50	266
pH-Average per station.	8.12	7.16	7.41	7.73
Turbidity-p.p.m. as silica	12	61	44	17

Lackey (1956) reported on a survey of Lytle Creek made in 1944. He studied the stream at five points which correlated well with the stations used later by Gaufin and other workers. He found 167 species of plant and animal plankton. Based on the relative abundance in the sampling stations of certain groups of species in them he concluded:

The environmental ranges of many microorganisms are wide enough for the organisms to be termed ubiquitous. But such organisms may reproduce rapidly enough to form blooms only within a narrow range of the critical factor, or combination of factors, which rarely occurs. Recent fecal pollution appears to be one such factor for certain species of the Euglenophyceae. The same environment appears to be limiting for some species of the Chrysophyceae.

Table VI presents a compilation of previously unpublished data provided by C. M. Tarzwell from information obtained by the aquatic biologists at the former Environmental Health Center, now the Robert A. Taft Sanitary Engineering Center, in a study of benthos samples taken during the week of December 6-13, 1949. It will be noted that under conditions of laboratory culture an entirely different picture of the bacterial population of the stream bed is obtained than when direct counts are attempted. However, both are necessary since each defines a different group of organisms.

The Geofungi of Lytle Creek.—To determine the relationship of fungi to the degree of pollution in a stream which receives effluent from a primary-type domestic sewage treatment plant, several techniques can be employed. One method permits the study of fungi associated with the zoo- and phyto-plankton as parasites of the living cells; another permits the isolation from the habitat of true aquatic fungi by means of hemp seed and other types of baits; another, the direct microscopic examination of the habitat to determine whether or not fungi are present; another permits determination from samples of the substratum of the amount of biological activity present by various physiological techniques; and finally samples of the habitat are treated as if they were soil samples, isolating from them by the use of suitable media such fungi as might grow well on this medium. In counting the different types of organisms in the plankton, no report was made of parasitic chytrids. Three sets of samples were baited with hemp seed in the laboratory with no especially significant results. In direct micro-

TABLE VI. Data on bottom deposits in Lytle Creek, week of Dec. 6-13, 1949

Category	STATIONS						
	7.6	7.2	6.5	5.2	4.2	2.8	1.0
	Riffles						
Water Temperature °F.....	32	42.8	41	35	32	34	51
Total Nitrogen as N ₂ -P.P.M.*.....	30	800	150	70	58	330	90
Total Phosphorus as PO ₄ -P.P.M.*.....	107	206	50	76.7	132	40.2	34.7
Volatile solids over total solids-%.....	39.2	49.6	23.7	32.3	36.1	24.1	6.87
Coliform M.P.N./sq. ft. Bottom area....	445M**	1367B	55.5B	55.2B	2.5B	257M	892M
Bacterial growth 20° C—48 hr. Billions M.P.N./sq. ft.....	765.2	13750.0	295	899	263	654	273M
Bacteria and fungi—Microscopic Count Millions/sq. ft.....	103.8		1476.9	315.6	35.6	4.23	0.63
Blue-green algae, Millions/sq. ft.*.....	3.75		4.66	13.18	152.17	8.45	1.26
Diatoms—Millions/sq. ft.....	611.9		2062.9	39.6	1135.04	351.82	69.93
Flagellates—Millions/sq. ft.....	11.25		5.83	5.64	54.7	107	17.62
Rhizopods and Ciliates—Millions/sq. ft..	2.5			1.88	1.37	1.41	
Pools							
Water temperature °F.....	32	42.8	41	35	32	34	51
Total Nitrogen as N ₂ —P.P.M.*.....	400	600	440	420			
Total Phosphorus as PO ₄ —P.P.M.*.....	52.3	364	306	86.5			
Volatile solids over total solids-%.....	9.05	47.9	43.4	10.8			
Coliform M.P.N./sq. ft. Bottom area....	.25M	1.02B	248M	46.5M	10.5M	2.48M	4.65M
Bacterial growth 20° C—48 hr. Billions M.P.N./sq. ft.....	120M	1.2B	4.65B	4.65B	248M	259M	465M
Bacteria and fungi—Microscopic count Millions/sq. ft.....	19.6		4802.16	49.78	4.5	2.03	
Blue-green Algae—Millions/sq. ft.*.....	1.82		348	97	5.41		
Diatoms—Millions/sq. ft.....	17.85		13.34	10.47	4.96	112.03	106.81
Flagellates—Millions/sq. ft.....	.46		109.3	159.25	8.56	95.2	71.2
Rhizopods and Ciliates—Millions/sq. ft..			8.93	8.89		22.4	.46

* Wet basis.

** M—Million; B—Billion.

Based on cells and cell clusters.

Note: Use of word "fungi" refers to *Sphaerotilus natans*.

scopic examination of benthos samples (Table VI), a record was made in terms of "bacteria and fungi—microscopic count, millions per square foot." From the comments accompanying the data it would appear that "fungi" in this instance referred to the "sewage fungus," *Sphaerotilus natans*, a filamentous bacterium. A purely physiological study of the activities of organisms in the benthos or plankton was not considered practical until something was known of the members of the population. Such a study would have involved the activities of many kinds of organisms in addition to fungi. It was hoped that the plating of habitat samples from each major habitat type in each zone, which had been analysed for other kinds of organisms, would yield information concerning the kinds and numbers of fungi occurring in the creek under various levels of change resulting from pollution.

The techniques used in the isolation of fungi from Lytle Creek samples have been described in earlier papers (Cooke 1954b, 1954c). The concern of the present report is to indicate that geofungi are present in the benthos and plankton of

a stream whether they be found in the water itself, in sediments in pools and riffles or even in the soil of the creek bank. In addition to listing the species which have been found, together with information about their occurrence in the various habitats of a stream (Table VII), their occurrence is summarized graphically in the accompanying histograms (Fig. 2 and 3).

In Table VII are listed most of the species of geofungi collected to date. The list includes 94 categories, among them certain collectives. In addition, members of 34 categories have been found only once in any one location and are not listed here. These include groups of cultures which have not been completely identified as yet. Thus the category "white yeasts" includes species in the genera *Candida*, *Cryptococcus*, *Torulopsis*, *Trichosporon*, and *Schwanniomyces*. The category "*Phoma* spp." includes what appear to be several species in addition to *Phoma terrestris*. There is a number of cultures which have not been identified beyond the families Moniliaceae and Dematiaceae because either they have never sporulated or their spore producing mechanisms have not yet

TABLE VII. Occurrence of fungi at sampling stations, Lytle Creek
(W = creek water; P = water and sediment in pools; R = water and sediment in riffles; S = bank soil)

Fungus	STATION								Sampling periods (of 12)
	1.0	2.8	4.2	5.2	6.5	7.2	7.6	8.7	
<i>Aspergillus versicolor</i>	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	10
<i>Fusarium aqueductum</i>	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	11
<i>Margarinomyces heteromorphum</i> ...	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	11
<i>Penicillium funiculosum</i>	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	12
<i>Penicillium lilacinum</i>	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	12
<i>Penicillium ochro-chloron</i>	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	12
<i>Penicillium variable</i>	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	11
<i>Pullularia pullulans</i>	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	10
<i>Rhodotorula glutinis</i> ss. lat.....	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	10
White Yeasts.....	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	WPRS	10
<i>Phoma</i> spp.....	WPRS	WPRS	WPRS	PRS	WPRS	WPRS	WPRS	WPRS	10
<i>Geotrichum candidum</i>	WPRS	WPRS	WPRS	PRS	WPRS	WPRS	WPRS	WPRS	12
<i>Cladosporium cladosporioides</i>	WPRS	WPRS	WPRS	WPRS	PRS	WPRS	WPRS	WPRS	10
<i>Trichoderma viride</i>	WPRS	WPRS	WPRS	WPRS	WPRS	PRS	WPRS	WPRS	12
<i>Penicillium</i> spp.....	WPRS	WPRS	WPRS	PRS	WPRS	PRS	WPRS	PRS	12
<i>Moniliaceae</i> spp.....	WPRS	WPRS	WPRS	WPRS	W RS	PRS	PRS	WPRS	10
<i>Dematiaceae</i> spp.....	WPRS	WPRS	WPRS	P S	W RS	P S	WPRS	WPRS	10
<i>Penicillium chrysogenum</i>	WPRS	WPRS	R	P S	W RS	WP	WP S	WPRS	3
<i>Coniothyrium</i> spp.....	WPRS	WPRS	W RS	WPRS	PRS	S	RS	W S	10
<i>Penicillium nigricans</i> (+nr.).....	WPRS	WPRS	RS	PRS	S	S	S	PR	7
<i>Fusarium oxysporum</i>	W RS	RS	W RS	PR	PRS	W R	PRS	RS	3
<i>Penicillium rugulosum</i>	W S	WP	RS	S	S	S	W S	S	1
<i>Aspergillus fumigatus</i>	PRS	WPRS	WPRS	WPRS	WP S	WPRS	PRS	WPRS	12
<i>Alternaria tenuis</i> ss. lat.....	PRS	WPRS	P S	P S	P S	WPRS	WPRS	S	10
<i>Aspergillus ochraceous</i>	PRS	RS	PRS	P S	PRS	P S	PRS	RS	10
<i>Gliocladium roseum</i>	PRS	WPRS	PRS	WPRS	P S	WPRS	PRS	P S	10
<i>Myrothecium verrucaria</i>	PRS	WPRS	WPRS	PR	RS	S	P S	S	10
<i>Penicillium herquei</i>	PRS	RS	PRS	S	P S	S	S	RS	8
<i>Penicillium oxalicum</i>	PRS	WPRS	WPRS	W RS	P S	WP S	PRS	PRS	11
<i>Penicillium fellutanum</i>	PR	R	P S	P	P S	S	P S	R	5
<i>Aspergillus flavipes</i>	RS	PRS	S	S	S	P S	P S	P S	9
<i>Mucor fragilis</i>	RS	PRS	PRS	WPRS	WPRS	WPRS	PRS	WP S	11
<i>Penicillium janthinellum</i>	RS	S	WPRS	WPRS	WP S	WPRS	WPRS	WPRS	9
<i>Penicillium purpureogenum</i>	RS	PRS	PRS	PRS	P S	RS	PRS	PRS	8
<i>Mucor plumbeus</i>	S	S	S	PRS	S	W S	P	W S	9
<i>Aspergillus niger</i>	WPRS	W RS	P S	WPRS		W S	RS	P S	12
<i>Penicillium puberulum</i>	WPR	PR	S		P S	P	RS	P	2
<i>Aspergillus sydowii</i>	WP S	W RS	PR		R	W R	P S	WPRS	4
<i>Penicillium martensii</i>	S	PR	P	S	P S	WP	P S		3
<i>Penicillium velutinum</i>	S	P	S	P S		R	S	P	1
<i>Coniothyrium fuckelii</i>	S	RS	P S	P		W S	RS	W S	3
<i>Mucor hiemalis</i>	S		P S	P S	S	S	S	S	3
<i>Mucor racemosus</i>	WP S		S	P S	P	W	W		3
<i>Fusarium solani</i>	W R	PR			PR	RS	RS	PRS	3
<i>Aspergillus clavatus</i>	PRS	S		P	P		PRS	PRS	7
<i>Penicillium expansum</i>	PR		RS		W	RS	P S	RS	3
<i>Paecilomyces varioti</i>	P S	W R		R	PRS		P	WPR	8
<i>Aspergillus terreus</i>	RS	RS	P S	RS			S	S	6
<i>Penicillium lanosum</i>	RS	RS	P S			RS	RS	RS	7
<i>Penicillium charlesii</i> (+nr.).....	S	S	W S	P			S	S	2
<i>Rhizopus arrhizus</i>			S	P	S	S	P	S	5
<i>Aspergillus flavus</i>	PR			S		W S	W S	S	5
<i>Penicillium javanicum</i> (+Ser.).....	P S		WP	S			P	W	2
<i>Epicoecum nigrum</i>	R		P		P	S		R	3
<i>Fusarium roseum</i>	R	P S	P S	W	S				2
<i>Stysanus stemonitis</i>	S			R		R	P	PR	1
<i>Zygorhynchus moelleri</i>	S	R			S		S	S	3
<i>Verticillium</i> spp.....		S	P S	S			W	W	3
<i>Thielavia</i> sp.....		S	P		S		R	W	1
<i>Aspergillus ustus</i>	WPR	S			P			PR	4
<i>Chaetomium funiculosum</i>	P		S		P	S			2
<i>Penicillium commune</i>	RS	W R	S		S				3
<i>Penicillium tardum</i>	R	RS			P			S	2
<i>Sphaeronema</i> spp.....			S	R		W	P		2

Table VII. (Continued)

Fungus	STATION								Sampling periods (of 12)
	1.0	2.8	4.2	5.2	6.5	7.2	7.6	8.7	
<i>Penicillium brevi-compactum</i>	WP	PRS		R					2
<i>Penicillium casei</i> (+nr.).....	W					W		W	1
<i>Gliocladium penicillatum</i>	P		P				P		3
<i>Pestalotia dichæta</i>	P	P						PR	1
<i>Fusidium viride</i>	R					R	R		1
<i>Monosporium olivaceum</i>	R				W S			S	1
<i>Penicillium cyaneo-fulvum</i>	S	W		P					2
<i>Penicillium raistrickii</i>	S	P S	R						2
<i>Mucor brunneus</i>		P	S	S					1
<i>Curvularia lunata</i>	/	RS			S		S		2
<i>Gliomastix convoluta</i>		S		S			PR		2
<i>Penicillium jensenii</i>			S		S		P		1
<i>Trichoderma alba</i>			S				P	P	2
<i>Humicola grisea</i>				P			RS	P	2
<i>Penicillium melinii</i>				S	W		S		2
<i>Penicillium parvum</i>					R		S	P	1
<i>Paecilomyces</i> sp.....	PRS						R		2
<i>Penicillium simplicissimum</i>	P S	P							1
<i>Penicillium aurantio-virens</i>	P		P						1
<i>Torula herbarum</i>	P	PRS							2
<i>Memnoniella echinata</i>	RS							R	3
<i>Mucor corticolous</i>	S							P	1
<i>Penicillium palitans</i>		R					S		1
<i>Aspergillus candidus</i>		S						S	2
<i>Aspergillus carneus</i>		S		P					2
<i>Paecilomyces marquandii</i>		S	WP						2
<i>Penicillium piscarium</i>		S						S	1
<i>Penicillium pulvillorum</i>		S			P S				1
<i>Aspergillus ruber</i>				P	R				2
<i>Penicillium citreo-viride</i>						S		RS	1

been observed accurately enough to complete an identification. Certain strains of *Penicillium* have not yet been identified to species or were discarded before identification was completed. In this table the categories are listed according to their occurrence in the stream. Thirty-five categories were found at least once in all 8 stations, while only 10 categories were found in all habitats sampled in all 8 stations.

The last column in Table VII indicates the number of times of the 12 sampling periods that the category listed was found at any point in the stream. We may arbitrarily assign these fungi to two of the categories adopted earlier (Cooke 1957b) for pollution fungi. None of the fungi found is *lymbiont*, restricted to a grossly polluted habitat. Those found in 5 or more sampling periods, according to Table VII, may be con-

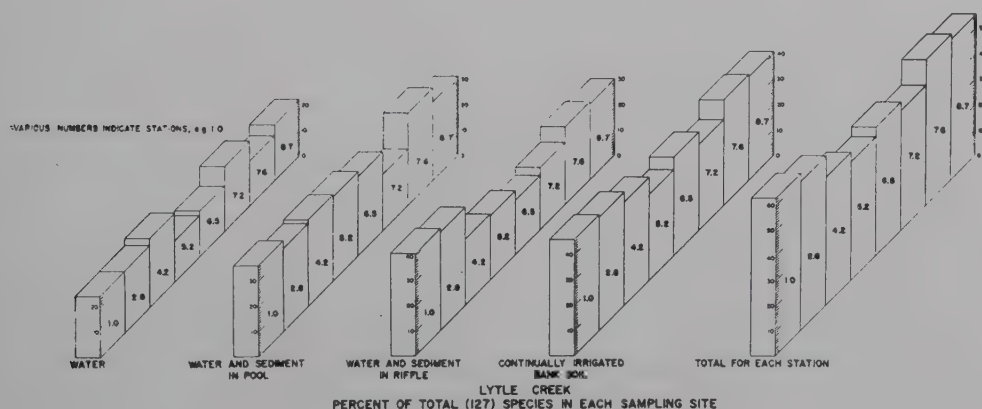
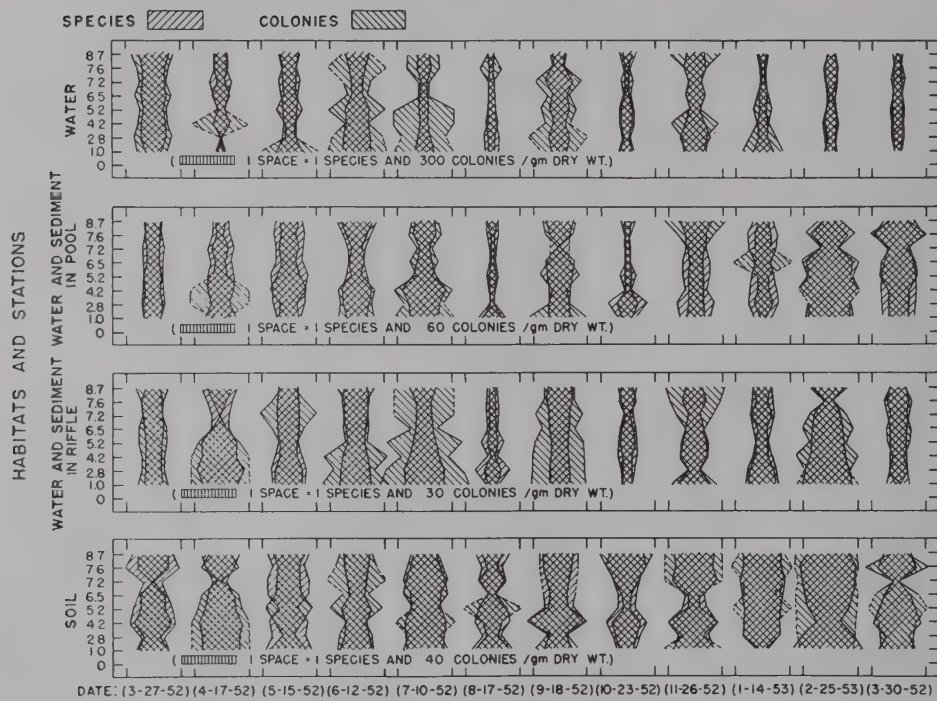


Figure 2.



LYTLE CREEK
NUMBERS OF SPECIES AND COLONIES OF GEOFUNGI AT EACH SAMPLING
STATION AT EACH SAMPLING DATE

Figure 3.

sidered *lymphiles*: species able to tolerate a pollution habitat as a livable one. Those species not tolerating such a habitat but only passing through, so to speak, are *lymaxenes*; they are the species found in fewer than 5 sampling periods. Since *lymphobes* cannot tolerate conditions of pollution, none was found in Lytle Creek, although some of the species found only once or twice, as a result of capturing a chance spore, may have been *lymphobes*. This analysis ignores the fact that a few species or categories were found only once and that some species were found more than once but in a portion of the stream still influenced to a small extent by upstream pollution. It is further assumed that those categories occurring 4 or fewer times have not become permanent members of the population, while those found 5 or more times have developed a continuity of existence within the series of environments which make up the sampling limits of the stream.

Figure 2 summarizes these data as a series of histograms based on the percentage of the total number of species categories present in any one

of the 32 sampled habitats. The first column represents those species found in water samples taken at the 8 stations, the second, those found in water and sediment in pools, the third, water and sediment in riffles, and the fourth represents those categories found in saturated bank soil always subject to the irrigative influences of the stream water and always flooded during periods of high water. The final column summarizes these data for each station.

For each station and each habitat the environment is in a continual state of flux. The stream is sufficiently small that the water is continually moving downstream and there is little chance for long periods of retention in backwater pools. During the late summer and autumn, and during periods of winter ice, water movement may be slow but during rainy periods the pools and riffles are continually scoured, although this action may be too mild to affect many of the animals which are present in an attached state. To a certain extent these features of water movement are reflected by the histograms in Figure 2.

Each set of histograms shows slightly different relationships between the species of fungi and their habitats. The water in the upper part of the stream carries a quantity of spores which is reduced as the stream passes the break in the trunk sewer line but which increases as the full load of the effluent of the sewage treatment plant is emptied into it. This variation is followed by a decline in numbers of species as the septic zone is passed. As oxygen supplies are increased, pollution loadings decreased and the full effects of enrichment are felt as the load of species is again increased.

It is apparent that an increase in nutrients entering the water and sediment in pools causes an effect on the fungus population. As the enrichment effects of the raw sewage from the trunk line sewer break are felt, populations increase, but at the point of outfall the number of species sharply declines. This condition is attributed to the highly septic conditions which affect only certain species, as colony counts demonstrate. Proceeding down stream, then, there is a gradual increase in the numbers of organisms which can adapt to waters carrying an increasingly mild load of fertilizing materials. At Station 2.8 the stream flows over flat limestone rocks providing little chance for development of sediments of the type sampled elsewhere.

The pattern in the riffles is similar to that in the pools except that the most severe influence of pollution is felt at Station 6.5 rather than at 7.2. Here there is a more rapid increase in number of species present after the zone of recovery is almost passed.

In the bank soil there is a good population of many species throughout the stream although this is depressed at two points. At Station 7.2 the depressing effect is explained on the basis of sewage outfall and accompanying septicity which is obvious as a deep soft layer of black mud. Some recovery is noted at Station 6.5 which is lost again at Station 5.2, beyond which recovery is noted along the length of the stream. The depression at Station 5.2 may be explained partly on the basis of habitat variation, although nothing in the habitat conditions appeared to account for this beyond the unaesthetic appearance and odor of the stream. It was a point in a stream in which a careful parent would not permit his children to play, to describe the condition qualitatively.

The depressing effect on the population of fungal species at Station 5.2 is again noted in the summary histograms which follow the pattern set up by the bank soil populations. Here is noted

the effect of the raw sewage entering at a point above Station 7.6 as well as the fertilizing effect on downstream populations of the sewage pollution received at Station 7.2.

In Fig. 2 no attempt is made to differentiate between seasons, the data presented being based only on the total number of species found in the stream. Fig. 3 presents information on a month-to-month basis for each of the four habitats at each of the 8 stations, comparing colony counts with numbers of species for each of the 32 habitats sampled. Here December is omitted but March is repeated; otherwise the pattern for a complete year is presented. Sampling stations are shown on the left of each of the four habitat types; sampling dates are given at the bottom of each of the 12 columns. Cross hatching for numbers of colonies runs from upper left to lower right; for numbers of species, from upper right to lower left. Usually the inner pair of enclosing lines includes the numbers of species for which one space on the scale indicates one species. The outer pair of enclosing lines usually includes the numbers of colonies for which one space represents 300 colonies per gram of dry weight of water, 60 colonies per gram of dry weight of water and sediment in pool, 30 colonies per gram of dry weight of water and sediment in riffles, and 40 colonies per gram of dry weight of water soaked bank soil.

This set of histograms illustrates a very definite reduction in numbers of species and colonies as a result of the added pollution in the stream at or just below the point of discharge of primary settled sewage. This effect is noted at Station 7.2 or Station 6.5 depending on the rate of flow of the stream water.

A quiet period in the life of the stream itself is demonstrated by relatively regular lines representing both species and colonies. Unusual disturbances such as special types of pollutional loadings, temperature conditions, precipitation conditions, or other causes result in moderate to strong variations in the shape of the curves enclosing the data for each sampling period involved.

DISCUSSION

Many kinds of fungi have become adapted to habitats such as may be found in streams. It has been shown (Cooke 1959a) that more than 90 species of soil fungi are adapted to the habitat of the surface film of the stones in low and high rate trickling filters and (Cooke 1959b) to all types of habitats in the trickling-filter-type sewage treatment plant. Natural streams have been subject to pollutional influences for as long as organ-

isms have lived along their reaches, a situation considered objectionable only during the last 50-100 yrs. It is suggested that soil fungi became adapted to the aquatic environment through their ability to break down organic pollutional matter. However, the postulation of such a thesis may be unnecessary since it is probable that soil fungi, finding their way into streams or sewage treatment plants, through run-off from the soil, washings resulting from flash floods, precipitation of spores from the air, and other ways have become adapted to these habitats by merely being bathed in an adequate supply of nutrients, which they incidentally aid in reducing to the mineral level.

Within the confines of the particular stream, Lytle Creek, between 8.7 and 1.0 miles above its mouth and below about 3 miles from its source, a large and varied population of soil fungi has been found. Few aquatic fungi of types usually sought by hemp-seed baiting techniques (Cooke and Bartsch 1959) have been found, and search has not been started for chytrids or aquatic Hyphomycetes. Based on these soil molds, it is suggested that a large population representing strains of at least 35 species has been found to occur at most of the sampling stations throughout most of the year, and that 10 of these have been found at all stations in 10, 11, and 12 of the 12 sampling periods.

The populations of soil fungi found in Lytle Creek add another example to the growing list of habitats to which fungi are known to be adapted. Here, in a completely aquatic habitat, these fungi are found, by means of pure culture techniques, to have joined the ranks of those scavenger organisms referred to by Whittaker (1957) as "reducers" and appear to be aiding in stream purification.

The occurrence of such fungi in aquatic environments could have been predicted since they have developed for students of aquatic fungi as culture contaminants ever since such fungi have been studied. Rather than interpret these as merely culture contaminants, it is emphasized here that they are definite members of the population, that they should be studied as such, and that their role in the habitat should be considered of fundamental importance in aquatic biology. Such fungi are capable of contributing to the reduction of B.O.D. in aquatic habitats, as has been demonstrated with 8 of the common species by Cooke, Moore and Kabler (1957). The same group of fungi is capable of using many kinds of carbohydrates and nitrogen sources without the addition of vitamin supplies, as has been demonstrated by Cooke (1957). While some of these fungi may

become nuisances and even undesirable organisms in human disease (Cooke and Kabler 1955) and in plant disease (Cooke and Kabler 1957), it seems apparent that as long as they are confined to an aquatic habitat where air-borne spores are produced at a minimum, they are contributing to stream purification by the reduction of organic waste materials through metabolic activities. Thus the same organism which may be detrimental to man's interests in one environment may be highly beneficial in another environment.

The activities of microorganisms in any environment may be overemphasized by one technique of study; underemphasized by another. To look for an accurate description of a fungus population with the use of a Sedgwick-Rafter cell or a Palmer Nannoplankton counting cell is to underemphasize that population, since few spores or thalli are readily apparent, while to rely solely on plate counts based exclusively on the techniques described above is to overemphasize this segment of the total biota. This is the import of a sentence in a recent evaluation of micro techniques by G. S. Wilson (1959) paraphrased as follows: "There are many faults and fallacies in microbiology such as overemphasis on the members rather than the nature of microorganisms in assessing the populations of microorganisms in any habitat."

Given the proper technique for sorting out the individual organism, the different groups of organisms, and the organisms with highly specialized requirements for nutrients or tolerances for microenvironments, each organism can be placed in its proper niche in the picture of the ecology of a stream. Until such techniques are available for geofungi, information can be developed in the laboratory concerning the role of each strain or group of strains in the environment. On this basis we may say that geofungi isolated from the water and stream-bed samples from Lytle Creek are contributing to the reduction of organic pollutants in that stream, and that they are probably contributing to the food supplies of larger organisms or of organisms higher in the food chain which may ingest them accidentally or intentionally.

SUMMARY AND CONCLUSIONS

The fungi found in the water and stream-bed samples of Lytle Creek habitats show a definite response to stream conditions resulting from pollution produced by direct dumping into the stream of raw sewage or of sewage which has passed through a primary-type sewage treatment plant. The creek receives raw sewage above the

treatment plant and this enrichment of the stream bed results in an increase in the fungus population below this accidental outfall. At the outfall of the treatment plant the populations of true fungi are depressed possibly as a result of septic conditions. They recover downstream and in the lower end of the creek, in the lower clean water zone, surpass the populations of the clean water zone above the treatment plant.

All habitats sampled in the stream and its bed were affected in a similar manner by the polluting materials. However, since the more common fungi found in the creek are self sufficient in all respects except that they are heterotrophic, it may be assumed that the fungi, at least the members of the permanent population, are contributing to the purification of the stream and its water as well as to the food supply of other organisms present in the habitat.

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INTERACTIONS BETWEEN ALPINE TUNDRA VEGETATION AND PATTERNED GROUND IN THE MOUNTAINS OF SOUTHERN NEW ZEALAND

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In the interior of the southern part of the South Island of New Zealand are several relatively low, flat-topped, fault block mountain ranges—the Dunstan Mountains, Carrick Range, Pisa Range, Rock and Pillar Range, Old Man Range, and parts of the Garvie Mountains. These schistose mountains appear deceptively gently-sloped and relatively low after viewing their steep and glacially eroded neighbors, the Remarkables and the Southern Alps. In spite of their lack of topographic distinction, the summit climates are as severe as any in New Zealand and are under strong Antarctic influence. As a result of the rigorous climate and the presence of extensive summit plateaus and ridges, the tops of these mountains are covered with a well-developed alpine tundra vegetation.

Typical of these tundra-capped mountains is the Old Man Range (Lat. 45° 20'S, Long. 169° 15'E), southwest of Alexandra, Central Otago. Griggs (1956), speaking of Mt. Washington (6,288 ft) in New Hampshire, U.S.A., says, "It is nothing much of a mountain, [yet] Mt. Wash-

ington has one of the worst of climates." Like Mt. Washington, the Old Man Range is not spectacular, yet its crest ridge has a climate far more severe than that of the surrounding country.

Unfortunately, there are few data to substantiate this. Until recently, no meteorological records existed for the Central Otago mountains. Climatic resums for the region have been based on valley stations such as Alexandra, some 5,000 ft below the 5,500 ft top of the Old Man Range. In Dec., 1958, A. F. Mark, for the Otago Catchment Board, set up two altitudinal series of weather stations on the Range, at the 1,000-ft contour lines and additional locations, from the base to the top. At this time, only one year's data are available (Mark 1959), but already it is evident that the upper part of the range receives much more snow and total precipitation than does Alexandra; the estimated mean annual precipitation at 5,200 ft in Fraser Basin is 77 in. vs. 13.2 in. at Alexandra. The crest is also much colder with an estimated mean annual temperature of 34° F for Fraser Basin as compared to 50.5° F for Alexandra.

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Alexandra itself is a characteristic station in the Inland South Island climatic province of Garnier (1958). This province is farthest from the sea of any place in the South Island, and therefore has a somewhat continental climate. There is greater difference between day and night temperatures and summer and winter temperatures than elsewhere in New Zealand. Winter minima down to 11° F and summer maxima up to 97° F have been recorded during 31 yrs of observations in Alexandra. During the 1959 winter, a minimum air temperature of 5° F was recorded at an elevation of 5,100 ft on the Old Man Range. In contrast to this, the Alexandra minimum for the same period was 19° F.

The region is semiarid because of its position in the lee of the Southern Alps and other ranges. Bright sunshine totals over 2,000 hrs per year, well above that of any of the surrounding coastal areas. Prevailing winds are northwesterly in summer and southwesterly in winter. The northwesterly is warm and usually dry, while the southwesterly is cold and often brings snow to the mountains during the passage of a cold front. Both winds may be quite strong.

The mountain crest appears to be subjected to very much higher wind velocities than is Alexandra. Spot readings of a northwesterly wind on the crest of the Range on 2 Feb. 1959 were in excess of 66 mph; the mean velocity for the same day in Alexandra was only 0.92 mph.

Snow and freezing temperatures occurred on the upper part of the Range during every month of the 1958-59 summer season, and often the fresh snow remained on the ground for several days. Semi-permanent snowbanks were still present at the end of summer (Mar.); in that respect also, the climate of the Old Man Range resembles that of Northern Hemisphere alpine regions in western North America and Europe.

Bright warm days occur on the Range but are much rarer than in the sunny dry weather of Alexandra because of the cap of low clouds which covers the mountaintop for days at a time. This cloud is a dense cold fog which keeps the temperature near freezing on many summer days when the valleys are in warm sunshine.

Garnier (1958), commenting on the lack of climatic data from the Central Otago mountains, states that these mountains (as evidenced by tree-line and mountain vegetation) very probably have a wetter and more severe climate than that of the surrounding valleys. This seems to be so.

GENERAL APPEARANCE OF THE SUMMIT REGION

The top of the Old Man Range is a broad undulating ridge of chlorite schist, the Otago

Schist of Upper Paleozoic and Lower Mesozoic age. Dotted over the summit plateau are resistant tors of this schist, some of them up to 50 or 75 ft high. These stand prominently over a bleak landscape of low matted alpine plants and occasional patches of large snow-tussock (*Danthonia flavescentis*).

A remarkable feature of this tundra is the nature of the soil surface which in many areas is made up almost entirely of either large hummocks or long parallel stripes. These stripe areas resemble huge plowed fields (Fig. 1). Together with the hummock areas, they cover hundreds of acres but are absent from parts of the wind-eroded summit backbone where the underlying schist outcrops. The stripes on the Old Man Range have been briefly mentioned by Cockayne (1928) and more recently, similar ones from the adjacent Garvie Mountains have been described by McCraw (1959).



FIG. 1. General view of a soil stripe area on crest of Old Man Range, Central Otago, showing appearance of alpine tundra vegetation.

Microtopography in the summit region is also characterized by large solifluction terraces, up to 2 m high. There are hundreds of these, some of which are apparently active. They are almost entirely on north- and northeast-facing slopes in the lee of the snow-drifting southwesterly winds of winter and facing the warm sun of spring.

The hummocks, stripes, and terraces all affect the pattern of the tundra vegetational mosaic. In turn, the microtopography itself appears to be partly the product of the vegetation. It is with these interrelationships that the present paper will deal. The field work was done largely during 1959.

HUMMOCKS AND STRIPES

The true hummock areas, as opposed to stripes, are almost level and occur on the top of the range to the north and south of the rocky highest

point. The hummocks range from about 20-40 cm high and are about 1-1.5 m in base diameter. At first glance, they resemble the frost hummocks of peat described from North America and Europe by Troll (1944), Hanson (1950), Billings and Mooney (1959), and others. However, instead of the ubiquitous *Carex* spp. of the northern hemisphere, these hummocks are almost entirely covered with low cushion plants typified by *Dracophyllum muscoides* and *Raoulia hectori*. Moreover, the hummocks do not consist of peat but of mineral soil.

The stripes appear to be greatly elongated hummocks. There is no readily apparent difference in vegetation pattern between stripes and hummocks, and the soil profiles across the stripes are essentially like those of the hummocks. Therefore, the vegetational and soil descriptions and analyses of these two forms of microrelief will be discussed together.

The stripes are confined to gentle slopes (4°-7°) as opposed to the near-level areas of hummock occurrences. On intermediate slopes (2°-3°), intermediate forms between hummocks and stripes are found. Stripes occur only on the west side of the summit ridge, and their orientation varies with the slope aspect. Almost all of the stripes occur on west- or southwest-facing slopes where they are oriented in a southwest-northeast direction. On some north-facing slopes, the stripes are oriented northwest-southeast.

Vegetational analyses of the hummock and stripe areas were made by point-intercept transects 10 m long with points at 5 cm intervals, making a total of 200 points per transect. Profiles of each transect were plotted on graph paper in the field. Two hummock stations, 3 stripe stations, and one intermediate station were sampled. Transects were run at right angles to stripe direction. The data for each station were

TABLE I. Composition of hummock and stripe vegetation based on transect data from 6 stations. T, S, and B designate tops, sides, and bottoms of hummocks and stripes, respectively

Species*	Life form	Symbol	Presence	% DOMINANCE			% DISTRIBUTION		
				T	S	B	T	S	B
<i>Drapetes dieffenbachii</i> Hook.	prostrate	Dd	2	2.11	1.04	0.44	58.4	29.7	11.9
<i>Raoulia hectori</i> Hook. f.	cushion	R	5	13.39	7.97	3.06	54.2	33.5	12.4
<i>Dracophyllum muscoides</i> Hook. f.	cushion	Dm	6	41.58	27.22	15.70	48.6	33.0	18.4
<i>Thamnia vermicularis</i> (Sw.) Schaer.	lichen	Tv	6	3.52	2.60	1.75	44.2	33.9	21.9
<i>Agrostis subulata</i> Hook. f.	small grass	As	6	2.11	2.60	1.31	34.6	44.0	21.4
<i>Poa colensoi</i> Hook. f.	small grass	Pc	5	2.11	2.95	3.06	32.7	47.1	20.2
<i>Celmisia ramulosa</i> Hook. f.	small shrub	Cr	1	1.41	0.69	1.31	40.8	20.9	38.2
<i>Polytrichum juniperinum</i> Hedw.	dwarf herb	Pj	6	1.41	2.43	1.75	29.8	44.4	30.8
<i>Celmisia laricifolia</i> Hook. f.	dwarf herb	Cl	5	1.76	1.21	1.75	37.0	26.4	36.6
<i>Luzula campestris</i> DC.	small grass	L	6	0.35	1.91	1.75	8.8	48.5	42.7
<i>Cetraria islandica</i> (L.) Ach.	lichen	Ci	5	2.46	11.44	14.40	8.6	41.3	50.2
<i>Celmisia viscosa</i> Hook. f.	medium herb	Cv	4	0.70	9.36	12.23	3.0	42.9	54.1
<i>Celmisia sessiliflora</i> Hook. f.	cushion	Cs	2	1.76	0.87	3.93	26.7	13.7	59.7
<i>Anisotome imbricata</i> Ckn.	cushion	Ai	1	0.70	—	—	—	—	—
<i>Alectoria nigricans</i> (Ach.) Nyl.	lichen	An	2	0.70	—	—	—	—	—
<i>Celmisia brevifolia</i> Ckn.	small shrub	Cb	1	0.70	0.17	—	—	—	—
<i>Phyllachne rubra</i> Cheesem.	cushion	Pr	3	0.35	1.04	—	—	—	—
<i>Trisetum spicatum</i> (L.) Richt.	small grass	T	3	0.70	0.35	0.44	—	—	—
<i>Anisotome aromatica</i> Hook. f.	small herb	Aa	2	0.35	0.17	0.44	—	—	—
<i>Abrotanella inconspicua</i> Hook. f.	cushion	A	4	0.35	0.69	1.75	—	—	—
<i>Drapetes lyallii</i> Hook. f.	cushion	Dl	2	0.70	—	1.31	—	—	—
<i>Coprosma pumila</i> Hook. f.	prostrate	Cu	1	0.35	—	0.44	—	—	—
<i>Lycopodium fastigiatum</i> R. Br.	small herb	Lf	1	—	0.17	—	—	—	—
<i>Euphrasia dyeri</i> Wettst.	small herb	E	1	—	0.17	—	—	—	—
<i>Craspedia uniflora</i> Forst.	small herb	Cf	2	—	0.35	—	—	—	—
<i>Hierochloa fraseri</i> Hook. f.	small grass	Hf	1	—	0.17	—	—	—	—
<i>Danthonia setifolia</i> (Hook. f.) Ckn.	small grass	D	1	—	1.04	—	—	—	—
<i>Hymenanthera dentata</i> v. <i>alpina</i> T. Kirk.	small shrub	Hv	2	—	1.39	0.44	—	—	—
<i>Celmisia argentea</i> T. Kirk.	cushion	Ca	2	—	0.35	1.75	—	—	—
<i>Gaultheria rupestris</i> R. Br.	small shrub	Gr	2	—	0.17	0.44	—	—	—
<i>Brachycome sinclairii</i> Hook. f.	small herb	B	1	—	0.17	0.44	—	—	—
<i>Cladonia</i> spp.	lichen	C	1	—	—	0.44	—	—	—
<i>Scleranthus biflorus</i> Hook. f.	cushion	S	1	—	—	0.44	—	—	—
<i>Phyllachne colensoi</i> Berggr.	cushion	Ph	1	—	—	0.87	—	—	—
Total vegetational cover				79.57	78.69	71.64			
Bare soil			6	3.87	3.12	3.06	38.2	31.8	30.0
Dead plants			6	16.21	17.50	12.65	34.5	38.6	26.9
Rock			5	0.35	0.69	12.65	2.6	5.2	92.2

* Voucher specimens of most of the species are deposited in the Herbarium of Duke University.

analyzed for percentage dominance (relative frequency of hits per species) and percentage distribution (relative frequency of hits for each species per microtopographic subdivision). The microtopographic subdivisions used were tops (T), sides (S), and bottoms (B) of the hummock-basin or stripe-furrow alternations. Since the number of intercepts was about twice as many on the sides as on the tops or bottoms, the distribution data from these latter two sites were weighted to provide values to be expected if an equal number of intercepts had been recorded in each of the 3 microtopographic sites. The individual station tables were quite similar and the data were therefore lumped and re-analyzed. The results are presented in Table I. Distribution data are shown in this table only for those species having dominance percentages exceeding 1% for each of two or more microtopographic subdivisions.

The life forms of the plants which were hit at 10 cm intervals were diagrammatically indicated on the profile for each transect. The life form categories used were: tall grass > 20 cm high, small grass < 20 cm high, medium herb > 10 cm high, small herb 5-10 cm high, dwarf herb < 5 cm high, cushion < 5 cm high, rosette < 5 cm high, prostrate herb < 2.5 cm high, and fruticose lichen. Figure 2 shows this type of bisect for Transect 2, a stripe area.

Cockayne (1928:319) graphically described the bitter, windy climates of the summit plateau of the Old Man Range and designated the vegetation as "South Island herb-moor." In our opinion, this "herb-moor" is truly an alpine tundra vegetation. Several typical tundra species*

* *Trisetum spicatum*, *Thamnolia vermicularis*, *Polytrichum juniperinum*, *Cetraria islandica*, *Luzula campestris*, *Alectoria nigricans*, *Solarina crocea*, and the very close congener of *Hieracium alpinum*, *H. fraseri*.

from the northern hemisphere are associated here with those of southern hemisphere derivation. It appears, therefore, to be the southern hemisphere equivalent of the arctic and alpine tundras of the north.

The dominant plant by far on the tops of the hummocks and stripes is the bronze-green *Dracophyllum muscoides*, the only other important plant being the gray *Raoulia hectori*. Both of these are cushion plants. The dominance is not so clear-cut on the sides. Here, *Dracophyllum* is still the principal dominant, but to a lesser degree, while secondary dominants are the fruticose lichen, *Cetraria islandica*, the medium herb, *Celmisia viscosa*, and *Raoulia hectori*, in that order. The bottoms of the protected intervals show even more floristic variety and the dominance of *Dracophyllum* is reduced to almost co-equal status with that of *Cetraria* and *Celmisia viscosa*. *Raoulia* is not prominent in the intervals.

Only about 7% of the ground on the tops and sides is bare or rocky. However, dead plants cover about 17% of the soil surface on these upper parts of the hummocks and stripes. In the intervals, there is a great increase in the amount of rock lying on the surface from less than one per cent (on the tops and sides) to almost 13% on the bottoms, with the result that the vegetation in the bottoms is more sparse than that on the sides and crests. This rock is mostly in the form of small flat stones a few centimeters wide. They are probably residual due to wind and water erosion. Possibly some of the small rocks may be deposited here by wind. In some places, rather large flat rocks (40-75 cm across) lie in the hummock intervals. However, not all intervals have them. The hummocks appear to have been built up between these large rocks and occasionally grow over them.

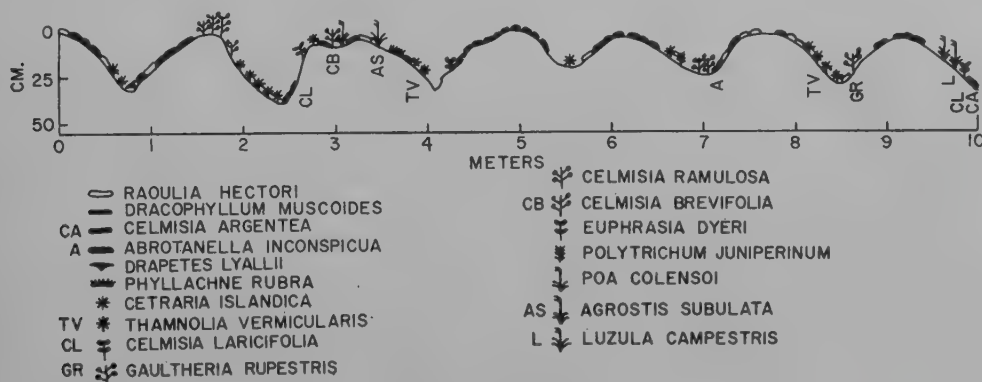


FIG. 2. Life-form bisect of Transect 2 across a soil stripe area at 5,280 ft elevation in the Fraser Basin, Old Man Range. The location is close to that of Figure 1. Vertical scale is twice the horizontal scale.

The percentage distribution data in Table I show that the component species can be sorted into 4 groups on a microtopographical basis: (1) those preferring hummock or stripe tops, (2) those found mainly on the sides, (3) those occurring principally in the furrow bottoms, and (4) those showing little or no site preferences. *Drapetes dieffenbachii*, *Raoulia hectori*, *Dracophyllum muscoides*, and *Thamnia vermicularis* are top-preferants. All are low plants, usually under 5 cm high.* *Agrostis subulata*, *Poa colensoi*, *Polytrichum juniperinum*, and *Luzula campestris*—one a large moss, and 3 with the small "grass" life-form—occur mainly on the sides. The principal furrow-bottom plants are the lichen, *Cetraria islandica*, and the medium herb, *Celmisia viscosa*. Plants of the latter species usually range from 10-20 cm in height. The non-preferants include the small shrub *Celmisia ramulosa* and the dwarf herb *C. laricifolia*.

Wind protection increases markedly from the top of the stripe to the bottom of the furrow even though the furrows usually run parallel with the prevailing wind. Wind protection and a decrease in evapotranspiration and increase in soil moisture in the furrow are probably the principal factors contributing to the steep species gradient in the 50-100 cm of slope between the crests and the bottoms of the basins or furrows.

On 2 April 1959, a sunny day with a constant light southerly wind, measurements of rate of air movement were made using a jewelled anemometer in a furrow, on the side of an adjacent stripe, at the top of the stripe, and 50 cm above the stripe. Ten one-minute readings were made in each location. The averages (in ft/min) are in Table II. The wind speed in the furrows was less than 7% of that recorded 50 cm above the crest of the stripe as compared to about 60% for the crest itself.

* See Whitehead (1954) for a discussion of relationships between growth form and wind exposure in the alpine tundra of Italy.

TABLE II. Wind velocity in ft/min in alpine stripe area on 2 April 1959. Weather fine, with light southerly wind. Averages of 10 one-minute measurements at each location

Location	(1) 50 cm above top of stripe	(2) top of stripe	(3) side of stripe	(4) bottom of interval
Average ft/ min.....	885.0	535.5	195.0	61.1
% of column 1....	100%	60.5%	22.0%	6.9%

While wind protection may be important for some furrow-bottom species, *Cetraria* is probably abundant there due to the frequent presence of free water. During the spring thaw at the end of October, 1959, standing water was present in the basins between hummocks. Water was also flowing down the furrows. In both cases, the upper limit of *Cetraria* coincided with the water line.

Cockayne (1928:319) describes the "peaty surface of the ground" in the hummock and stripe areas of the Old Man Range. These hummocks do superficially resemble the peat hummocks of the northern hemisphere tundra. However, soil profiles dug across the hummocks and stripes quickly dispel this illusion. Peat was absent from every one of the several profiles dug during this work. No peat was seen anywhere in the stripe and hummock areas. Instead, a well-developed set of mineral soil horizons exists with the A horizon darkened by the presence of humus, but completely lacking in peat.

Soil profiles in 3 stripe or hummock areas were mapped to scale in the field. Large composite soil samples were taken from each horizon in each of the profiles. These samples were air-dried for several weeks in the laboratory and then analyzed mechanically by sieving. The silt and clay were separated from the 0.05 mm fraction for two profiles by dispersing duplicate samples of 50 g of soil in 100 ml of water with 5 ml of 1N NaOH and 5 ml of a saturated solution of $\text{Na}_2\text{C}_2\text{O}_4$ and allowing the suspension to stand for one hour. At that time, the suspension was decanted and the precipitate dried and weighed as silt. The material remaining in suspension was considered to be clay and the amount of clay was obtained by difference. Loss-on-ignition values were determined by igniting duplicate samples of oven-dry 2 mm fraction soil in a muffle furnace. Volume-weight was approximated by pouring 100 cc uncompacted 2 mm fraction into a 100 cc graduate and then weighing the soil. Soil analysis data are in Tables III and IV.

A soil profile across a stripe in Transect 2 is shown in Figure 3. This profile is typical of other stripe and hummock profiles except that the downward extension of the A horizon at the crest is unusual. This anomaly is probably related to the presence of a small shrub at that point. The dark-brown sandy loam A horizon varies from 5-20 cm or more in thickness. This horizon is usually thickest at the crest of a hummock or stripe and thinnest in the furrow. The A horizon's dark color is due to the much higher organic content (12-16%) as compared to that

TABLE III. Soil analyses. Transects 1 and 2 are from stripe areas, Transect 8 is from a hummock area, Transect 3 is from a solifluction terrace.

Area	Horizon	MECHANICAL ANALYSIS (sizes in mm) (% of total wt)									% Loss on ignition	Volume wt* g/cc
		over 4.76	4.76-	2.0-	1.2-	0.6-	0.3-	0.15-	0.076-	under 0.05		
TS.1...	A	3.35	3.35	2.47	2.76	2.09	5.22	24.88	19.18	36.69	14.41	0.63
TS.1...	B	7.77	7.17	4.50	4.37	2.89	6.97	20.27	10.16	33.96	5.77	1.00
TS.1...	C	62.37	10.11	5.19	3.91	2.31	3.16	5.97	2.61	4.44	3.61	1.16
TS.2...	A	0.10	3.68	5.44	3.84	1.90	3.88	22.26	14.16	44.74	15.93	0.65
TS.2...	B	15.83	9.38	5.47	5.05	3.32	4.36	16.57	9.68	30.49	6.01	0.99
TS.2...	C	48.87	7.96	3.94	3.26	1.90	2.47	8.46	6.08	17.07	4.31	1.03
TS.8...	A	1.56	7.69	4.99	4.70	2.75	5.03	23.78	15.98	36.53	11.90	0.805
TS.8...	B	15.18	10.03	6.42	5.82	3.49	7.79	13.75	10.49	30.07	4.77	1.00
TS.8...	C	47.77	13.32	7.56	2.02	.91	1.59	7.24	6.03	16.56	3.66	1.00
TS.3...	Upper rocky	24.50		8.52	7.11	4.33	7.76	12.80	9.82	28.48	6.19	0.97
TS.3...	Lower non-rocky	6.07	3.97	2.47	3.73	3.20	6.28	17.98	13.46	43.15	4.82	0.90

* On disturbed 2 mm fractions.

TABLE IV. Soil textural analyses of 2 mm fractions. Transect 1 is from a stripe area, Transect 8 is from a hummock area

Location	% sand	% silt	% clay	textural type*
TS. 1-A horizon.	60.7	27.3	15.0	sandy loam
TS. 1-B horizon.	59.1	37.7	3.1	sandy loam
TS. 1-C horizon.	83.9	15.2	0.9	loamy sand (rocky)
TS. 8-A horizon.	61.0	28.6	10.3	sandy loam
TS. 8-B horizon.	59.8	37.5	2.7	sandy loam
TS. 8-C horizon.	57.5	38.5	4.0	sandy loam (rocky)

* After Alexander, L. T. (1952). The physical nature of soil. Agron. 2: 1-23.

of the light-brown B horizon (4-6%). The B horizon ranges from 10-40 cm thick and is much thicker under the stripe or hummock than in the intervals. The top of the rocky C horizon is practically horizontal and there is a sharp discontinuity between it and the relatively rockless B horizon. The outstanding characteristic of the C horizon is the abundance of flat schistose rocks up to 10 or 15 cm in diameter and considerable fine gravel and coarse sand. This strongly contrasts with the A horizon which is made up primarily of finer sands. The B horizon is intermediate in texture, but resembles the A horizon much more closely than it does the C.* As McCraw (1959) found under stripes in the Garvie Mountains, the soils resemble those of the Kairoua series of Gibbs, Raeside, *et al.* (1945).

* Rockless soil stripes, similar in all details except that the rocky C horizon is replaced by permafrost, occur on the slopes near Nunavak Lagoon on the northern coastal plain of Alaska not far from Barrow (Lat 71°N). There, too, the lichen *Cetraria islandica* grows in the furrows between the stripes (personal communication, E. E. C. Clebsch).

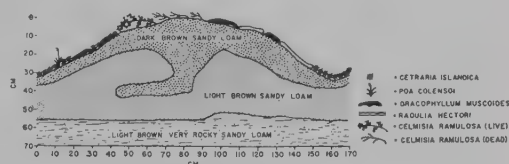


FIG. 3. Soil profile through a stripe in the area of Transect 2, Fraser Basin. The dark brown sandy loam is equivalent to an A horizon, the light brown sandy loam to a B horizon, while the light brown very rocky sandy loam is the partially disintegrated parent material or C horizon. The downward extension of the dark brown soil is an anomaly probably due to the roots of *Celmisia ramulosa* on the crest of the stripe.

SOLIFLUTION TERRACES

The solifluction terraces are in the form of broad steps, several meters to many meters across the top. They occur on north- and northeast-facing slopes exceeding 7°.

At least one of the terraces is now active as evidenced by sod and rocks being pushed off the



FIG. 4. Front of large solifluction terrace near crest of Old Man Range. This terrace is active, but moving slowly.

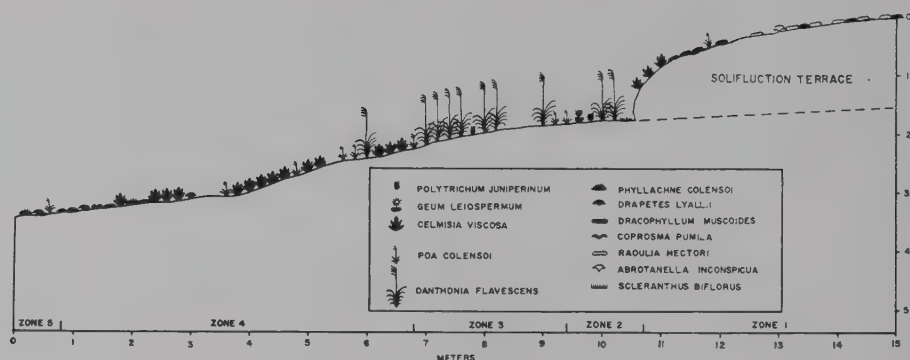


FIG. 5. Life-form bisect of a typical solifluction terrace showing the 5 vegetational zones. The break between the *Danthonia flavescens* in Zone 3 and the *Celmisia viscosa* of Zone 4 is particularly well-marked.

face and whole plants being over-ridden and incorporated into the terrace at the crack near the base. The face of this terrace is shown in Figure 4.

Transects were surveyed over 3 terraces; the profile of each terrace was plotted to scale on graph paper in the field and point-intercepts were recorded at 10 cm intervals. Life-form bisects of these terraces were reconstructed from these data; one of these is shown in Figure 5. The

vegetational data from all 3 terrace transects have been analyzed together and are in Table V.

Since the fronts of the terraces face away from the prevailing southwesterly winds of winter, snowdrifts are produced at least as deep as the height of the terrace. On 1 July, 1959, when the snow depth in the alpine zone was generally about 3 ft, the tops of the larger solifluction terraces for a distance of 15-20 ft back from the face were bare of snow, and were almost the only snow-free

TABLE V. Vegetational analysis across three solifluction terraces. Zone 1=top of terrace, Zone 2=face plus immediate lee, Zone 3= mid-lee, Zone 4=far lee, Zone 5=beyond usual lee effects

Species	Symbol	Life form	% DOMINANCE					% DISTRIBUTION				
			1	2	3	4	5	1	2	3	4	5
<i>Raoulia hectori</i>	R	cushion	17.53					100.				
<i>Drapetes dieffenbachii</i>	Dd	prostrate	5.25					100.				
<i>Trisetum spicatum</i>	T	small grass	2.06					100.				
<i>Celmisia argentea</i>	Ca	cushion	1.03					100.				
<i>Phyllachne rubra</i>	Pr	cushion	3.09					100.				
<i>Abrotanella inconspicua</i>	A	cushion	1.03				2.86	50.0				50.0
<i>Dracophyllum muscoides</i>	Dm	cushion	24.74			3.77	42.86	53.3			13.3	33.3
<i>Luzula campestris</i>	L	small grass	4.12			1.38	2.86	57.1			28.5	14.2
<i>Danthonia flavescens</i> Hook. f.....	Df	tall grass		31.25	60.00	20.13			12.3	48.1	39.5	
<i>Celmisia viscosa</i>	Cv	medium herb	3.09	6.25	25.16			6.6	4.4		88.8	
<i>Celmisia haastii</i> Hook. f.....	Ch	small herb		12.50				100.				
<i>Geum leiospermum</i> Petrie.....	G	small herb		3.13				100.				
<i>Scleranthus biflorus</i>	S	cushion		3.13				100.				
<i>Carex</i> sp.....	C	small grass		6.25	1.54				66.6	33.3		
<i>Gnaphalium</i> sp.....	Gn	small herb			1.54					100.		
<i>Celmisia prorepens</i> Petrie.....	Cp	medium herb			1.54					100.		
<i>Coprosma pumila</i>	Cu	prostrate				0.63					100.	
<i>Drapetes lyallii</i>	Dl	cushion		6.25		3.14	5.71		22.2		55.5	22.2
<i>Poa colensoi</i>	Pc	small grass	4.12		6.15	16.98	2.86	11.1		11.1	75.0	2.7
<i>Polytrichum juniperinum</i>	Pj	dwarf herb		21.88	16.92	9.43	2.86		20.5	32.3	44.1	2.9
<i>Raoulia grandiflora</i> Hook. f.....	Rg	dwarf herb		3.13	3.08	1.38	2.86		16.6	33.3	33.3	16.6
<i>Hectorella caespitosa</i> Hook. f.....	H	cushion				0.63	2.86				50.0	50.0
<i>Phyllachne colensoi</i>	Ph	cushion				0.63	5.71				33.3	66.6
<i>Celmisia sessiliflora</i>	Cs	cushion					2.86					100.0
Total vegetational cover.....			66.06	93.77	90.77	83.26	74.30					
Bare soil.....			5.15	3.13	7.69	5.03	8.87		4.5	22.7	36.3	13.6
Dead plants.....			14.43	3.13	1.54	11.32	11.43	36.8	2.6	2.6	47.3	10.5
Rock.....			14.43			0.63	5.71	82.3			5.8	11.7

areas visible. The snowdrift area in the lee of each face was packed up to the top of the face. This latter condition prevailed for the remainder of the winter.

Since these drifts melt slowly in the spring and summer, they provide a source of low temperature and soil moisture against the drying effects of the summer northwesterlies. The result is that the lee of every terrace is occupied by a continuum of plants either of much taller life form or less drought-resistant than those occupying the tops of the terraces. Inspection in the field and analysis of the data indicate fairly distinct breaks in continuum composition at certain places along the gradient. This made it possible to divide the terrace transect data into 5 zones, as follows: Zone 1, top of terrace; Zone 2, face of terrace and immediate lee to a distance equal to the height of the terrace; Zone 3, the mid-lee extending from the outer edge of Zone 2 to a distance of 3 times the height of the terrace; Zone 4, the far-lee from the outer edge of Zone 3 to a distance of 8 times the height of the terrace; and Zone 5, beyond a distance of 8 times the height of the terrace. This latter zone appeared to be beyond most lee effects.

Table V shows relative dominance in each zone and the distribution of individuals of each species from zone to zone. Zone 1 is dominated by small prostrate herbs or cushion plants (principally *Dracophyllum muscoides* and *Raoulia hectori*), almost all of which are confined to that zone. A few of these species reappear in Zone 5 or the outer edges of Zone 4 where the snowdrifting effects of the terrace are minimal. Zone 2 is dominated by the tall *Danthonia flavescens* (snow-tussock) with an understory of *Polytrichum juniperinum*. The characteristic snowbank plant, *Celmisia haastii*, is confined to this zone. Zone 3 is almost completely dominated by *Danthonia flavescens*; almost half of the *Danthonia* occurring along the transect is in this mid-lee zone. The principal dominant in Zone 4 is *Celmisia viscosa*, although there is considerable *Danthonia* and *Poa colensoi* present. Almost all of the *Celmisia viscosa* occurs in this zone; this *Celmisia* belt in the far-lee is well-marked in the field. Zone 5, like Zone 1, is dominated by cushion plants with *Dracophyllum muscoides* by far the most important one.

A soil trench was dug through the face of the large terrace shown in Figure 4 and the soil profile plotted to scale. This profile is illustrated in Figure 6. The upper 130 cm of the terrace depth is made up of rocky medium-brown sandy loam resting on a relatively non-rocky yellow-

brown loam which has a clayey texture. The upper edge of this lower horizon has a uniform dip, corresponding with the general slope, of about 12°. The uppermost rocky layers of the terrace are apparently moving downhill at a slow rate, held in check by the turf on the front of the terrace. This front is bulged out over a crack near the base where the terrace is overriding the lower terrace-front vegetation. Rocks, soil, and sod are breaking off the front where it approaches the vertical and this debris falls to form a miniature talus slope at the foot of the bank and over the non-rocky subsoil. The similarity between the profile of this bank and those illustrated by Warren Wilson (1952:260, 261) from Jan Mayen Island at 71° N Lat in the Greenland Sea is striking. Hanson (1950) describes similar terraces from Alaska, and Johnson and Billings (1960) report them from the Beartooth Plateau of Wyoming. McCraw (1959) mentions terraces from the Garvie Mountains of Central Otago. Analyses of soils from the rocky and non-rocky layers of soil in the profile shown in Figure 6 are listed in Table III.

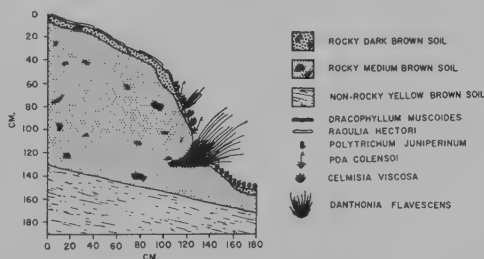


FIG. 6. Soil profile through the front of the large solifluction terrace shown in Figures 4 and 5. The large *Danthonia* in the crack near the base is being buried by the advance of the terrace.

Some of the smaller solifluction terraces are made up of stripes whose main axes are at angles of between 75° and 85° with the front of the terrace. These stripes do not appear to be different from the soil stripes described in the previous section and the vegetation is of the same type and shows the same stripe-furrow alternation. A photograph across the top of one of these terraces appears in Figure 7.

A dissection was made of a stripe-terrace and the soil profiles sketched in the field. The soil appears to consist of A and B horizons similar to those of normal stripes, but somewhat more rocky. In this latter respect, the stripe-terraces resemble ordinary terraces.

The terrace-stripes may be 20-30 m long; they are oriented in a northwest-southeast direction



FIG. 7. View across the top of a stripe-terrace near crest of Old Man Range. The abundant plant in the nearest furrow is *Celmisia viscosa*; the dominant cushion plants on the stripes are *Dracophyllum muscoides* (dark) and *Raoulia hectori* (light).

while the terraces face more nearly north. In almost every respect, the stripe-terraces appear to be intermediate between the stripes and the ordinary solifluction terraces. They appear to be moving very slowly, if at all.

DYNAMICS OF VEGETATION-MICROTOPOGRAPHY RELATIONSHIPS

How the Old Man Range hummocks have formed is not known for certain. They superficially resemble the peat hummocks of the arctic and alpine regions of the northern hemisphere. However, the northern peat hummocks are built up by a combination of peat accumulation and the upthrusting of silt and rocks from below by intense soil frost action, generally over permafrost (Billings and Mooney 1959: Fig. 1). The Old Man Range hummocks, however, do not consist of peat, there is no indication of rocks being upthrust under the hummock-centers from the almost level upper boundary of the C horizon, and permafrost is absent.

McCraw (1959) believes that the hummocks and stripes on the adjacent Garvie Mountains have been formed by a common process, but that this process is not one known to occur under present environmental conditions. He thinks that the hummocks and stripes are now stable and are not forming under the present climate, but were formed during a previously, colder cycle.

It would appear that these hummocks take a very long time to build up. The sharp discontinuity between the rocky, coarse C horizon and the relatively non-rocky, fine-textured B horizon and the lack of rock intrusion into the latter precludes formation by intense deep soil frost action (congeliturbation). Frost action is probably involved in formation of the hummocks, but it is

superficial and on a "micro" basis similar to the needle ice ("piprake") effects described by Troll (1944), Gibbs, Raeside, *et al.* (1945), and Gradwell (1957). This type of diurnal rather than seasonal frost action can produce surface soil stripe patterns in alpine soils of tropical and subtropical mountains, and is characteristic of such regions which lack permafrost.

Peat accumulations may once have been present in the hummock areas (Cockayne 1928) but none are there now, and it is doubtful whether peat was ever abundant enough to be important in hummock formation. Moreover, the *shape* of the hummock is determined by an accumulation of sandy loam A and B horizons resting on a level C horizon foundation from which the two upper horizons are sharply differentiated in texture. This combination of a rock-free mineral soil hummock or stripe with a rocky C horizon foundation from which it is sharply separated in texture suggests 3 possible physical origins for the hummocks: (1) accumulation of wind-blown soil in old snow-tussock clumps or in cushion plants, (2) polygonal frost-heaving due to relatively shallow annual freezing *above* the rocky C horizon and additional sorting on the hummock crests due to diurnal needle ice, or (3) a combination of wind accumulation and shallow annual and diurnal frost-sorting. Of the 3 possibilities, the last seems the most likely.

The hummocks are sometimes very regularly spaced in all directions, like trees in an orchard. It is difficult to see why such a regular spacing would result from sand and silt accumulation under cushion plants alone. Every small cushion would seem to have an equal chance of forming a hummock. This would result in small hummocks close together, which is not the case. The spacing of the hummocks is about the same as is found in a near-virgin stand of snow-tussock. This similarity in spacing may be merely coincidental, the result of polygonal surficial frost-sorting. On the other hand, if wind deposition is involved in hummock formation, it is possible that individual snow-tussock plants were responsible for the original trapping and accumulation of wind-borne material. Although snow-tussocks at present are relatively scarce and apparently of relict status in the alpine zone of the Range, they almost certainly occurred in greater abundance in the past. The soil profiles of hummocks and stripes on adjacent mountains have been described by a pedologist (McCraw 1959) as being similar to that of Kaikoura loam (Gibbs, Raeside *et al.* 1945), typically developed under snow-tussock vegetation. It is now impossible to determine

when, or if, snow-tussock vegetation was destroyed in the alpine zone of the Range. Relatively recent destruction is suggested by the persistence of occasional relict tussocks close to the summit today and the occurrence of tussock stands on adjacent but less accessible mountains of similar elevation.

Beginning about 100 yrs ago, with the arrival of the European settlers, snow-tussock was burned indiscriminately throughout the mountains of the South Island with the intention of improving the forage for stock. However, presumably more than 100 yrs would be required for the dwarf alpine vegetation to reach its present well-established condition in view of the severe environment, plus the impact of a new retarding factor, grazing by sheep. Perhaps alpine vegetation replaced snow-tussock which had been eliminated as a result of pre-European fires of Maori origin. Possibly this succession may have been assisted by the postulated 13th century climatic deterioration in the South Island (Raeside 1948, Holloway 1954). Rigorous environmental conditions could have prevented the re-establishment of snow-tussock in the present alpine zone without the microenvironmental control of a dense tussock cover. A striped microtopography does occur associated with snow-tussock vegetation today on a severely wind-swept slope near the summit of the Tararua Range, North Island (Zotov *et al.* 1936:269, Fig. 5). According to Zotov, the wind has eroded numerous narrow channels in the ground with the intervening strips covered with snow-tussock. Unfortunately, no soil profile descriptions are presented. Without this, the possible role of snow-tussock as a contributing agent in the origin of stripes and hummocks on the Old Man Range cannot be substantiated.

Whether or not the presence of snow-tussock was involved in the formation of the hummocks, it is still possible that they are at least partially wind phenomena. The distribution of the mineral soil fractions and rocks in the hummocks, the sharp discontinuity at the top of the C horizon, and the lack of frost thrusting of large rocks from below all indicate that *deep and severe freezing* is not the cause of hummock-formation. Spring observations in October and November, 1959, do indicate, however, that the A and B horizons of the stripes and hummocks are frozen seasonally. The thawing pattern is similar to that in tundra peat hummocks of the northern hemisphere but there is an apparent lack of frost in the C horizon.

Diurnal freezing and thawing, perhaps accompanied by needle ice, during the snow-free

season certainly causes some frost-heaving and sorting of small stones polygonally into the basins between hummocks. Such sorting could also produce alternating soil and stone stripes on slopes. The stone stripes, being slightly lower, could become channels. In the channels, erosion caused by meltwater or rainwater would tend to accentuate the differences between soil stripe and channel. The accumulation of wind-blown fine material in the cushion plants on the crests of the stripes above the erosional rills might also contribute to the differentiation. In spite of the high winds of the summit region, the soil now is seldom dry enough to blow in quantity. Therefore, it seems likely that surficial frost-sorting has been the dominant factor in hummock and stripe formation and that wind-deposition has been of secondary importance. The continuing accentuation of the hummocks and stripes is probably due to an environmental combination of surficial frost-sorting, wind erosion and deposition, and rill erosion.

Since the stripes have essentially the same soil profile and vegetation as the hummocks, it is reasonable to assume that stripe-formation is essentially the same process as hummock-formation with the added effect of slope. The intermediate stripe-hummock areas described earlier may provide one clue to the origin of the stripes. Two quadrats, each 6 m on a side, were mapped in the intermediate area. One of these maps is reproduced in Figure 8.

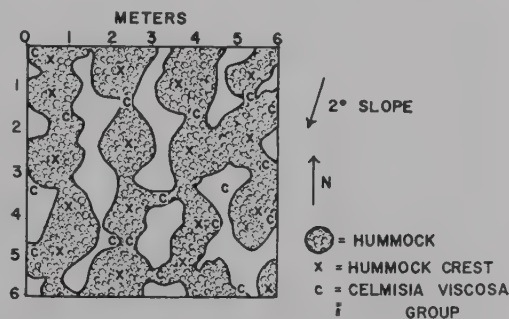


FIG. 8. Map of a quadrat in a "beaded" hummock area which is transitional between hummocks and stripes. Note the even distribution of the hummock crests and the positions of the *Celmisia viscosa* "lin'ages."

It is apparent that these stripes are "beaded," that is, they are made up essentially of regularly distributed hummocks which are beginning to connect up primarily in one direction, with a secondary, incomplete connection, at an angle of about 45° from the main direction of connection. The hummocks tend to connect up in a down-

slope direction; in this case, toward the southwest. Two factors appear to be involved, slope and wind-direction. It is difficult to separate them here since the main component of each is southwesterly. However, angle and direction of slope are certainly involved in the coalescing since the hummocks tend to remain distinct on relatively level areas. The direction of the coalescing (and thus of the resultant stripes) appears to be in that 45° line of regularly spaced hummocks which is nearest the direction of the combination of slope direction and prevailing wind direction. Prevailing wind direction can be determined roughly by the wind-erosion scars on the tops of some hummocks. In the illustration in Figure 8, the resultant stripe direction is just about north-south. In other places, it tends somewhat more southwest-northeast. But in almost every case, the stripe areas are on west or southwest-facing slopes. The coalescence of the hummocks into stripes, then, appears to depend upon a combination of slope direction and wind direction.

The actual linkage may be due in part to the drifting and settling of wind-blown mineral soil into colonies of *Celmisia viscosa* which occur in the intervals between the hummocks. *Celmisia*, a relatively large-leaved herb, does not occur in all the hummock-intervals, but usually in the shallower ones in the lee of the prevailing wind (Fig. 8). The *Celmisia* plants appear to accumulate wind-blown soil and to grow upward with the accumulation. When the linkages get high enough, the *Celmisia* is apparently exposed to wind-blast and dies out. The cushion plants, *Dracophyllum muscoides* and *Raoulia hectori*, could then take over, and stripe formation could be completed by the development of erosional channels and surficial frost-sorting. Smaller, secondary *Celmisia* linkages occur along the nearest 45° diagonal, where wind and slope are still partially right for stripe formation, but these secondary linkages seldom get very high because of the greater frequency with which the prevailing wind blows through the main furrows and possibly because they are cut through by runoff from meltwater or rain.

It is likely also, that surficial frost-thrusting on the downhill sides of hummocks would tend to create linkages between hummocks. Most linkages of hummocks into stripes might be the result of both such frost-thrusting and wind-deposition of fine soil particles.

Whatever the cause, when the stripes are mature, the result of this furrowed microtopography on the alpine vegetation is to produce a regular

alternation between the wind-resistant and relatively drought-tolerant cushion plants of the stripe crests and the more sensitive plants restricted to protection of the furrows. Figure 9 illustrates snow protection of the furrows during the spring snow-melt period. This situation is analogous to the position of the drier drifting snow of autumn and winter.



FIG. 9. Snowmelt pattern in a stripe area in spring showing snow protection in furrows.

DEGRADATION OF HUMMOCKS AND STRIPES

In general the hummocks and stripes appear to be stable and covered with intact vegetation but there are places where they are being disintegrated by wind action. This degradation starts when wind undermines damaged or dead plants at the top of a stripe or hummock. The trigger factor for degradation could be overgrazing or trampling in a susceptible area, or it could be drought and resultant snow-blast in a relatively dry windy winter.

There are places near the crest of the range where this disintegration has occurred and is occurring at present. Most of the damage appears to have occurred in the past. Cockayne described it more than 30 yrs ago (Cockayne 1926:320). When disintegration does take place, the stripes or hummocks usually are leveled down to the top of the rocky C horizon. Sometimes, however, enough small rocks are present in the A and B

TABLE VI. Vegetational composition (% dominance) along a 20 m transect from undisturbed hummocks to severely deteriorated hummocks

Species	Life form	No apparent deterioration			Slight deterioration			Severe deterioration		
		T	S	B	T	S	B	T	S	B
<i>Danthonia setifolia</i>	small grass	—	10.2	—	—	—	—	—	—	—
<i>Hymenanthera dentata</i> v. <i>alpina</i>	small shrub	—	—	5.6	—	—	—	—	—	—
<i>Celmisia viscosa</i>	medium herb	—	6.8	5.6	—	—	—	—	—	—
<i>Polytrichum juniperinum</i>	dwarf herb	—	5.1	—	—	—	—	—	—	—
<i>Agrostis subulata</i>	small grass	20.0	1.7	—	—	1.9	—	—	—	—
<i>Poa colensoi</i>	small grass	—	6.8	5.6	—	—	6.3	—	—	—
<i>Raoulia hectori</i>	cushion	20.0	20.3	22.2	—	3.8	—	3.1	2.1	7.5
<i>Thamnia vermicularis</i>	lichen	—	1.7	5.6	—	—	—	3.1	—	2.5
<i>Cetraria islandica</i>	lichen	—	6.8	27.8	—	—	—	—	1.4	—
<i>Luzula campestris</i>	small grass	—	1.7	—	—	—	—	—	1.4	—
<i>Anisotome aromatica</i> v. <i>lanuginosum</i>										
T. Kirk.....	small herb	—	—	—	5.3	—	—	—	—	—
<i>Dracophyllum muscoides</i>	cushion	40.0	23.7	—	36.8	38.5	—	43.8	39.2	37.5
<i>Abrotanella inconspicua</i>	cushion	—	—	—	—	1.9	—	—	1.4	2.5
<i>Celmisia laricifolia</i>	dwarf herb	—	—	—	—	1.9	—	—	0.7	—
<i>Hectorella caespitosa</i>	cushion	—	—	—	—	—	—	3.1	3.6	5.0
<i>Anisotome imbricata</i>	cushion	—	—	—	—	—	—	0.7	—	—
<i>Hebe hectori</i> (Hook. f.) Ckn. and Allen.....	small shrub	—	—	—	—	—	—	0.7	—	—
<i>Phyllachne rubra</i>	cushion	—	—	—	—	—	—	0.7	—	—
Total vegetational cover.....		80.0	84.8	72.4	42.1	48.0	6.3	53.1	51.9	55.0
Dead plants.....		20.0	15.3	22.2	21.1	17.3	50.0	15.6	22.1	35.0
Bare soil.....		—	—	5.6	36.8	25.0	43.7	15.6	15.0	2.5
Rock.....		—	—	—	—	9.6	—	15.6	10.7	7.5

horizons to act as a residual erosion pavement, thus preventing complete loss of the soil.

A 20 m permanent transect was set up in a hummock deterioration area about $\frac{1}{2}$ mile north of Old Man Rock and marked by aluminum posts. On this transect, the northernmost 5 m showed no apparent deterioration, the next 4 m showed slight deterioration of the hummock tops, and the southernmost 11 m were severely deteriorated and the hummocks almost completely blasted away. The vegetational composition in terms of percentage dominance for these 3 zones is shown in Table VI.

As deterioration proceeds and the hummocks are leveled, there is a sharp loss of individuals of *Agrostis subulata* and *Raoulia hectori* from the hummock tops and sides, and of *Celmisia viscosa* and *Cetraria islandica* from the lower sides and bottoms. There is a great increase in bare soil and rock and only *Dracophyllum muscoides*, of the original vegetation, remains undiminished in percentage of ground covered in the severely wind-eroded area. Actually, it has increased its coverage somewhat because it now occupies the wind-scoured former furrows where *Cetraria islandica* and *Celmisia viscosa* have all but disappeared and *Raoulia hectori* is much reduced in coverage. The susceptibility of *Raoulia* to this more rigorous environment as compared to *Dracophyllum* is surprising, since both are extremely

flattened cushion plants. The characteristic species of the severely deteriorated areas are 3 miniature cushion plants: *Hectorella caespitosa*, *Anisotome imbricata*, and *Phyllachne rubra*.

FORMATION OF SOLIFLUCTION TERRACES

The solifluction terraces are the result of flow of waterlogged soil downslope over a substratum of somewhat different consistency. Figure 6 shows the clear-cut difference between the two layers. Under the present climate, the lower layer is not frozen "tjäle," as it would be under such terraces in the Arctic. Some terraces do appear to be active, although probably not as much as at some past time, and the sod on the face is enough to keep the movement very slow.

The formation of these terraces is difficult to relate to events in the recent past, although Gibbs, Raeside *et al.* (1945) describe small accelerated terraces as the result of tussock destruction by fire and grazing. The terraces in the Old Man Range appear to be older, considerably higher, and slow-moving. The flattish areas back of the terrace tops, where ground cover of cushion plants is sparse, tend to become waterlogged and gelatinous in the spring. This material is subject to flow on the slopes and tends to build up into terraces held in check by sod on the face of the terrace. It is doubtful that the whole depth of the terrace flows at the same rate. The upper-

most soil flows far more rapidly; it is this soil which pushes the sod off the face to form a miniature talus which in turn becomes buried by new debris from the top of the face.

In some places, as mentioned earlier, the terraces seem to be formed by the coalescence and flowage of typical raised stripes. For a while, at least, each stripe maintains its own tongue-like extension on the advancing terrace face. Eventually, these tongues lose their individuality and the front of the terrace becomes relatively uniform. These small stripe-tongues are not to be confused with larger lobes, 5-15 m across, which are often found on the terrace fronts. These latter lobes are apparently due to differential flow on steeper or diverging slopes or over wetter places.

The relationship between stripes and terraces is difficult to detect. Apparently, however, these stripes are the same as described earlier. Under certain conditions of warming, waterlogging, and critical slope, however, they may start to move downhill slowly. During this process they pick up some rock from the underlying C horizon and increase in height. Eventually, the stripe-terraces may evolve into full-fledged terraces in which the stripes no longer are apparent.

As the terrace grows higher at the face, the snow-drift effect in the lee becomes more pronounced. Into this protected, more moist area, migrates a species whose individuals cannot tolerate the rigorous microclimate of the open wind-swept tundra: *Celmisia haastii*. Here also, *Danthonia flavescens* finds a suitably moist and protected site. Simultaneously, the top of the terrace, just back of the face, is becoming more exposed to wind force, and therefore more rocky, as the front of the terrace becomes relatively higher. With such increased exposure, as a result of snow loss by wind, scattered cushions of *Dracophyllum muscoides*, *Raoulia hectori*, and *Phyllachne rubra* dominate the sparse vegetation. In the far lee of the terrace at a distance from the face of more than 8 times its height, this low cushion-plant community is repeated, but because of slightly more wind protection, it is somewhat better developed and covers a greater percentage of the ground.

SUMMARY

The alpine tundra vegetation of the Old Man Range, South Island, New Zealand, is marked by the abundance of 3 types of microtopographical features: soil hummocks, raised soil stripes, and solifluction terraces. Several quantitative vegetational transects were mapped in each of the types. Soil trenches were dug, the profiles plotted to scale, and soil samples taken for analysis.

The vegetations of the hummocks and stripes are similar. *Dracophyllum muscoides* and *Raoulia hectori*, low cushion plants, dominate the exposed crests, and, to a lesser extent, the sides and bottoms of the intervals and furrows. In the latter location, they share dominance with the lichen, *Cetraria islandica*, and the medium-herb, *Celmisia viscosa*.

Soil profiles in the hummocks and stripes show sandy loam A and B horizons with few rocks lying over a level, coarse-textured, rocky C horizon. There is no evidence of deep and intense frost thrusting action in the formation of either the stripes or hummocks. Rather, it is postulated that they are primarily the result of a combination of surficial frost-sorting, wind deposition, and rill erosion by water.

Intermediate areas between hummocks and stripes indicate that the stripes may sometimes originate by deposition linkages between hummocks in a downhill direction toward the prevailing winter southwesterly winds, or rarely toward the summer northwesterly winds. *Celmisia viscosa*, growing in the lee of hummocks, provides the catchment for wind-blown soil to form the linkages. Surficial frost-sorting, flowage of waterlogged hummock soil, and rill erosion are also involved in the change from hummock to stripes.

Degradation of hummocks and stripes by wind erosion has occurred in some places near the crest of the range. The trigger factor is either overgrazing and trampling, or drought, or a combination of these. Both dead and living plants at the tops and sides of the hummocks and stripes are undermined by the wind which carries sand and snow as blasting agents. In serious cases, the soil of the hummocks and stripes is completely eroded away, leaving the rocky surface of the C horizon exposed and populated, only by scattered miniature cushion plants.

Some of the solifluction terraces appear to be active at present. The terraces occur on north- and northeast-facing slopes and produce extensive snowdrifts in their lees, away from the southwesterly winds. The vegetation developing in the snowdrift area shows a continuum from the base of the terrace to a distance in the lee equal to about 8 times the height of the terrace. This continuum is typified close to the face by *Celmisia haastii*, *Geum leiospermum*, and *Danthonia flavescens*, farther out by *Danthonia* and *Celmisia viscosa*. The top of the terrace and the region beyond the principal snowdrift effects are occupied by cushion plants, mainly *Dracophyllum muscoides* and *Raoulia hectori*.

Sections through the terrace fronts show vertical faces from the tops of which rock, soil, and plants are being pushed. There is an infolding of living plants into the terrace at a crack near the base. The upper layer of soil ranges from 20 cm to 1.5 m deep, depending on the size of the terrace, and is somewhat dark and rocky. This upper layer is apparently moving over a clay-like non-rocky lower layer whose upper boundary slopes downhill at an angle corresponding to that of the general slope (about 12°).

Some small terraces appear to be the result of movement downhill of coalesced typical raised soil stripes. How this movement of the stripe-terraces originates is not known.

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SOME INTERRELATIONS OF SAGEBRUSH, SOILS, AND GRAZING INTENSITY IN THE NORTHERN GREAT PLAINS¹

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The group of plants called sagebrush (*Artemisia* spp.) includes many species which vary widely in site adaptability, growth form, longevity, and palatability to livestock. These plants comprise a substantial portion of the vegetation on many

western rangelands, and often characterize the landscape over wide areas. Information is limited on the influence of soils, soil characteristics, and grazing on distribution and abundance of even the more common species of *Artemisia*. This paper reports a study of the effects of grazing rates and soil differences on abundance and growth characteristics of *Artemisia tridentata* and *A. cana*, two of the important sagebrush species in the Northern Great Plains.

¹ Study initiated by the former Northern Rocky Mountain (Now Inter-mountain) Forest and Range Experiment Station, U. S. Forest Service, Missoula, Montana. Conducted as part of a cooperative study with Montana Agricultural Experiment Station and Animal Husbandry Research Division, Agricultural Research Service.

These species differ in several important characteristics. The high competitive ability of big sagebrush (*A. tridentata*) with grass vegetation is well known (Blaisdell 1949, Frischknecht and Bleak 1957), but that of silver sagebrush (*A. cana*) is little understood.

Both species are affected by drought and grazing, but silver sagebrush may resprout after drought or grazing injury while big sagebrush does not (Ellison and Woolfolk 1937).

Both species provide nutritious forage, particularly during winter. Cook *et al.* (1954) indicated that on the winter ranges of Utah big sagebrush meets the requirement of pregnant ewes for protein, phosphorus, and carotene, being below requirements only in energy, and that this species is normally a significant portion of sheep diet. Cole (1956) reported that big sagebrush, silver sagebrush, and fringed sagewort (*A. frigida*) make up the bulk of the diet of antelope for 8 months of the year in eastern Montana.

Van Dyne in his investigations at the U. S. Range Livestock Experiment Station (1959) found high use of silver but not of big sagebrush by steers during the winter. Utilization was usually as high as or higher than that of black greasewood (*Sarcobatus vermiculatus*) and often higher than that of winterfat (*Eurotia lanata*), shrubs well known for high palatability.

Several investigators have studied the influences of and interaction between soils and grazing on big sagebrush in different parts of the West (Stewart *et al.* 1940, Cooper 1953, Evanko and Peterson 1955, Marquiss and Lang 1959). These indicated that heavier rates of grazing favored this species. Thatcher (1959) noted the marked effect of soil differences on distribution of this species.

Reed and Peterson (in press) indicated that heavy rates of stocking favored silver sagebrush during the late 1930's and early 1940's at Miles City, Montana, but abundance of big sagebrush was reduced.

Because of the value of silver sagebrush as winter and emergency forage in the Great Plains, and the generally limited density and abundance of both species there as compared with other areas, some authorities question whether they should be considered undesirable except on local areas (Platt 1959).

EXPERIMENTAL AREA

The study area is about 6 miles south of Miles City, Montana. It is in the more arid portion of the Northern Great Plains with lower forage production and less abundant mid-grasses than in the

Dakotas and the more moist part of the Canadian area.

The precipitation, topography and soils are fairly typical of the southwestern portion of this plains region. Topography of the study area is primarily gently sloping benchlands to nearly level bottoms, although rough breaks and dry watercourses define part of the relief. Soils vary from nearly pure clays to sandy clays and sandy loams.

Vegetation varies from a dense cover of many species in areas largely dominated by blue grama grass (*Bouteloua gracilis*) on the lighter soils to sparse, practically pure stands of big sagebrush and Sandberg bluegrass (*Poa secunda*) on the more clayey soils. Other abundant species are western wheatgrass (*Agropyron smithii*), needle-and-thread-grass (*Stipa comata*), buffalo grass (*Buchloe dactyloides*), Threadleaf sedge (*Carex filifolia*), silver sagebrush, fringed sagewort, and plains pricklypear (*Opuntia polyacantha*).

Precipitation was recorded at the headquarters of the U. S. Range Livestock Experiment Station approximately 6 miles northwest of the study area.

The study sites were located on two pastures which had been heavily grazed and two which had been lightly grazed by Hereford cattle since 1932. These pastures, described by Holscher and Woolfolk (1953), were used only during summer between May 15 and late October. They are included in a long-term grazing intensity study which has been partly reported by Reed and Peterson (in press).

The heavily grazed pastures were grazed at an average stocking rate of 1.85 acres/animal unit month from 1949-1959, the period of study. During this time the stocking rate varied from a low of 4.11-3.94 acres/A.U.M. in 1949 to 1.46-1.44 in 1955.

On the two lightly grazed pastures average stocking rates were 3.14 and 3.53 acres/A.U.M., ranging from 8.03-7.03 acres in 1949 to 2.76-2.47 in 1955.

During the study average utilization by weight of western wheatgrass, a co-dominant, ranged from 49.5% on the most heavily grazed pasture to 31.0% on the most lightly grazed one. Utilization of blue grama averaged 23.6 and 12.3%, respectively.

METHODS

On these experimental pastures 30 plots, each 10 x 12 m, were established in the mid-30's. At this time each pair of plots was matched as closely as possible in adjacent heavily grazed and lightly

grazed pastures on the bases of similar vegetation cover and soil.

During mid-summer of 1949, 1955, 1957, and 1959 all big and silver sagebrush plants were counted and average crown diameters and plant heights were measured on the experimental plots. The crown diameters were classed as Class I, less than 5 cm in crown diameter; Class II, between 5 and 10 cm in crown diameter; and Class III, more than 10 cm in diameter. Average height of the 5 tallest shoots or stems was measured from ground level in 10 cm classes.

Plot data were compiled separately by 3 of the major soil groups recognized by Gieseke (1948): upland, slope, and terrace. There were no plots on bottom and undifferentiated soils. In the upland soil group plots were on Fort Collins light loam (9 in. of friable light loam, 6 in. compact loam, 18 in. mass. cal. silt loam, 10 in. mass. silt loam) and on an unnamed loam soil similar to the above. On the slope soils plots were on Grail silty clay loam (7 in. friable silty clay loam, 8 in. prismatic cal. silty clay loam, 18 in. blocky cal. loam).

More plots were on soils of the terrace group than any other. These included an eroded phase of an unnamed clay (one in. cal. clay mulch, 19 in. mass. cal. clay, 10 in. mass. clay—lime flecked), Beckton silty clay loam (slick spots, saline, $\frac{1}{4}$ in. gray crust, 2 in. claypan, 2 in. platy silty clay, 9 in. mass. cal. silty clay), and Nunn silty clay (one in. clay loam crust, 8 in. mod. heavy clay, 6 in. mass. cal. silty clay, 9 in. mass. cal. silty clay loam).

These soil groups largely conform to recognized range sites (U. S. D. A. 1956). Plots on the upland soils group were confined to silty sites. The plots on the terrace soils group were located about equally on two sites, dense clay and pan spots.

PRECIPITATION

During the study, growing-season and annual precipitation averaged 86% of the 82 yr mean. In only 3 of the 11 yrs did both precipitation values exceed the long-time average (Table I).

RESULTS

Plant Numbers

The number of plants of big sagebrush was more influenced by soils than by grazing intensity (Table II). On the upland soils a small but consistently greater number of plants was present under the heavy stocking rate than under the light. This differential effect was not evident on the terrace soil group up to 1957, but in 1959

TABLE I. Seasonal (April 1-October 1) and annual precipitation at Headquarters of U. S. Range Livestock Experiment Station, 1949-59

Year	Seasonal- Precipitation	Annual- Precipitation
	<i>Inches</i>	
1949.....	4.25	7.68
1950.....	7.67	10.67
1951.....	9.90	12.23
1952.....	5.29	7.80
1953.....	9.68	13.53
1954.....	8.04	9.42
1955.....	10.33	13.07
1956.....	8.19	10.34
1957.....	10.08	13.45
1958.....	7.48	12.59
1959.....	7.30	10.88
11-year avg.....	8.02	11.06
82-year avg.....	9.28	12.90

there were considerably more plants under light stocking on these soils.

Silver sagebrush populations were influenced in an opposite manner by soils and grazing intensity (Table II). Although plant numbers were only about 10% of those of big sagebrush throughout the period, there were 5 to 30 times as many plants under light grazing as under heavy. There were no plants on any of the heavily grazed plots in 1949. By 1959 plant numbers had increased on both upland and terrace soils, but the increase was more rapid under light stocking than under heavy.

No big or silver sagebrush plants were observed on experimental plots on the slope soils at any time, although a few plants of both species were present outside the plots in 1957 and 1959.

TABLE II. Calculated number of big sagebrush and silver sagebrush plants per acre by year, grazing intensity, and soil group

Soil group and grazing intensity	Year			
	1949	1955	1957	1959
	<i>Number per acre</i>			
	<i>Big sagebrush</i>			
<i>Upland soils</i>				
Heavy grazing....	1106	1025	1430	1443
Light grazing.....	701	668	816	890
<i>Terrace soils</i>				
Heavy grazing....	5659	3530	3723	4364
Light grazing.....	5234	3507	3676	5827
	<i>Silver sagebrush</i>			
<i>Upland soils</i>				
Heavy grazing....	0	121	135	121
Light grazing.....	94	277	594	701
<i>Terrace soils</i>				
Heavy grazing....	0	27	13	20
Light grazing.....	105	361	425	449

Crown-Class Distribution

The crown-class distribution of big sagebrush (used as an index to age-class distribution) varied both by soils and by stocking rate (Table III). There were distinctly smaller proportions of class I crowns (seedlings) under the lighter stocking on the upland soils. However, on the terrace soils there were no differences between stocking rates. The proportion of plants in this class decreased between 1949 and 1959 on both soils under both stocking rates.

TABLE III. Average percentage of big sagebrush plants by year, grazing intensity, crown class, and soil group

Soil group, crown class, and grazing intensity	YEAR			
	1949	1955	1957	1959
	<i>Per cent</i>			
<i>Upland soils</i>				
Class I ¹				
Heavy grazing . . .	16.5	7.2	9.0	7.0
Light grazing . . .	12.5	0	0	1.5
Class II ¹				
Heavy grazing . . .	31.7	13.8	21.2	15.4
Light grazing . . .	29.8	5.1	20.7	14.4
Class III ¹				
Heavy grazing . . .	51.8	79.0	69.8	77.6
Light grazing . . .	57.7	94.9	79.3	84.1
<i>Terrace soils</i>				
Class I ¹				
Heavy grazing . . .	20.1	5.5	0.2	2.0
Light grazing . . .	19.8	10.7	0	1.0
Class II ¹				
Heavy grazing . . .	36.0	19.4	5.2	4.9
Light grazing . . .	30.4	22.5	1.3	6.4
Class III ¹				
Heavy grazing . . .	43.9	75.1	94.6	93.1
Light grazing . . .	49.8	66.8	98.7	92.6

¹ Crown class I—0 to 5 cm., II—5 to 10 cm., III—10 + cm.

There was a consistently greater proportion of class III crowns (mature plants) of big sagebrush under light stocking on the upland soils. On these soils there was an over-all slight increase in this group under both stocking rates. On the terrace soils there was little or no difference between stocking rates, but the proportion of plants in this crown class increased more rapidly on these soils than on the upland soils.

The proportion of plants of big sagebrush in crown class II (young plants) decreased on both soils under both stocking rates between 1949 and 1955-57. No marked differences were observed between soils or stocking rates.

The crown-class distribution of silver sagebrush was more erratic than that of big sagebrush (Table IV). On the upland soils the proportion of plants in crown class I remained low under the lighter grazing intensity. Under heavy grazing no plants were present on the plots until

TABLE IV. Average percentage of silver sagebrush plants by year, grazing intensity, crown class, and soil group

Soil group, crown class, and grazing intensity	YEAR			
	1949	1955	1957	1959
	<i>Per cent</i>			
<i>Upland soils</i>				
Class I ¹				
Heavy grazing . . .	0	0	20.0	22.2
Light grazing . . .	7.1	12.2	3.4	12.5
Class II ¹				
Heavy grazing . . .	0	38.9	20.0	16.7
Light grazing . . .	35.7	24.4	31.8	19.2
Class III ¹				
Heavy grazing . . .	0	60.1	60.0	61.1
Light grazing . . .	57.1	63.4	64.8	68.3
<i>Terrace soils</i>				
Class I ¹				
Heavy grazing . . .	0	0	0	0
Light grazing . . .	17.9	4.2	0	35.0
Class II ¹				
Heavy grazing . . .	0	71.4	0	60.0
Light grazing . . .	42.9	2.1	3.5	35.0
Class III ¹				
Heavy grazing . . .	0	28.6	100.0	40.0
Light grazing . . .	39.2	93.7	96.5	30.0

¹ Crown class I—0 to 5 cm., II—5 to 10 cm., III—10 + cm.

1957 and 1959 when the proportion of plants in this class increased to approximately double that under the light stocking rate.

On the terrace soils there were no crown class I plants under the heavy stocking. Under the lighter grazing the proportion of plants in this class slowly decreased from 1949 to 1957 and then sharply increased.

The proportions of silver sagebrush plants in crown class III were considerably greater under light stocking on the upland soils from 1949 to 1955 and on the terrace soils from 1949 to 1957. After those dates the proportions of plants of this crown diameter were similar under both stocking rates. From 1957 to 1959 the proportion of plants in this class remained constant on the upland soils, but decreased rapidly on the terrace soils.

The proportion of plants of this species in crown class II was erratic on both soils, but perhaps more so on the terrace soils. No distinct differences were evident between the two stocking rates or between soils.

Height-Class Distribution

The height-class distribution of big sagebrush reveals trends by years, soils, and grazing intensities (Table V). On the upland soils there was a distinct trend under heavy stocking for a continuous decrease in the proportion of plants less than 10 cm high and an increase in the proportion

over 30 cm. Under the light rate of stocking this trend was also evident, but not as distinct. Under the light stocking rate the corresponding decreases in the shorter plants and increases in taller ones were more erratic and most clear for those plants under 10 cm and over 40.

TABLE V. Average percentage of big sagebrush plants by 10-centimeter height class, grazing intensity, year, and soil group

Soil group, year, and grazing intensity	MIDPOINT OF 10-CENTIMETER HEIGHT CLASSES							
	5	15	25	35	45/	55	65	75
<i>Upland soils</i>								
1949	<i>Per cent</i>							
Heavy grazing...	46.3	28.0	17.7	6.1	1.2	0.6	0	0
Light grazing...	27.9	31.6	19.2	12.5	4.8	1.0	0	0
1955								
Heavy grazing...	29.6	21.7	17.1	14.5	10.5	4.6	2.0	0
Light grazing...	15.2	26.3	16.2	19.2	10.2	12.2	1.0	0
1957								
Heavy grazing...	33.0	21.7	13.7	16.0	7.5	6.6	0.9	0.5
Light grazing...	6.6	36.4	15.7	8.3	20.7	8.3	4.1	0
1959								
Heavy grazing...	16.8	24.8	18.7	15.0	14.0	7.9	2.8	0
Light grazing...	6.8	25.8	13.6	16.7	20.5	11.4	5.3	0
<i>Terrace soils</i>								
1949								
Heavy grazing...	67.2	27.6	7.2	0.9	0	0	0	0
Light grazing...	60.5	31.4	7.4	0.6	0	0	0	0
1955								
Heavy grazing...	47.5	28.0	19.5	4.0	1.1	0.1	0	0
Light grazing...	51.0	26.1	17.4	4.8	0.7	0	0	0
1957								
Heavy grazing...	33.3	32.2	22.3	8.2	3.7	0.4	0	0
Light grazing...	16.9	42.9	30.7	7.7	1.4	0.2	0	0
1959								
Heavy grazing...	11.2	45.2	31.2	9.4	2.9	0	0	0
Light grazing...	7.5	52.5	30.5	8.0	1.2	0.2	0	0

On the terrace soils these trends were also continuous and even more uniform. The decreases on these soils under both stocking rates took place in the less than 10 cm height class and the increases in the over 10 cm classes.

There were several observable differences in height-class distribution of big sagebrush between grazing rates on the upland soils. In all sample years there were distinctly smaller proportions of plants less than 10 cm high on the lightly stocked areas than on the heavy, and there was a trend, most evident in 1949, for more of the taller plants—over 10 cm high—on these lightly stocked areas.

On the terrace soils the height-class distribution of big sagebrush was similar under both stocking rates. Only in 1957 was there much difference between the rates, and then there were fewer plants under 10 cm and more plants between 10 and 30 cm high under light stocking.

The height-class distribution of silver sagebrush like the crown-class distribution was more

erratic and variable than that of big sagebrush (Table VI). There was a complete absence of plants less than 10 cm high under heavy stocking on the terrace soils, and a progressive decrease in this height class up to 1957 under light stocking on the upland soils. There was a distinct trend for a greater proportion of plants in the over 40 cm high classes under light stocking on both soils.

TABLE VI. Average percentage of silver sagebrush plants by 10-centimeter height class, grazing intensity, year, and soil group

Soil group, year, and grazing intensity	MIDPOINT OF 10-CENTIMETER HEIGHT CLASSES											
	5	15	25	35	45	55	65	75	85	95	105	
<i>Upland soils</i>												
<i>Per cent</i>												
1949												
Heavy grazing.....	0	0	0	0	0	0	0	0	0	0	0	0
Light grazing.....	28.6	28.6	0	0	28.6	14.3	0	0	0	0	0	0
1955												
Heavy grazing.....	16.7	50.0	22.2	11.1	0	0	0	0	0	0	0	0
Light grazing.....	14.6	29.2	26.8	14.6	4.9	4.9	4.9	0	0	0	0	0
1957												
Heavy grazing.....	35.0	25.0	35.0	5.0	0	0	0	0	0	0	0	0
Light grazing.....	4.5	45.4	22.7	12.5	5.7	2.3	2.3	0	0	0	0	0
1959												
Heavy grazing.....	11.1	33.3	22.2	33.3	0	0	0	0	0	0	0	0
Light grazing.....	8.7	46.2	20.2	7.7	12.5	1.9	1.9	1.0	0	0	0	0
<i>Terrace soils</i>												
1949												
Heavy grazing.....	0	0	0	0	0	0	0	0	0	0	0	0
Light grazing.....	75.0	10.7	0	7.1	0	0	0	3.6	3.6	0	0	0
1955												
Heavy grazing.....	0	85.7	14.3	0	0	0	0	0	0	0	0	0
Light grazing.....	2.1	51.0	44.8	0	0	0	0	0	2.1	0	0	0
1957												
Heavy grazing.....	0	50.0	50.0	0	0	0	0	0	0	0	0	0
Light grazing.....	47.8	41.6	5.3	1.8	1.8	0	0	0.9	0	0	0.9	0
1959												
Heavy grazing.....	0	60.0	40.0	0	0	0	0	0	0	0	0	0
Light grazing.....	53.3	40.0	2.5	0.8	0.8	0.8	0	0	0.8	0	0.8	0

DISCUSSION

Due to irregular sampling dates and widely varying annual precipitation, it is difficult to ascertain the effects of weather on populations of the two sagebrush species. The decade was generally drier than the previous one, and the first sampling year, 1949, was one of the driest on record. The continuous effects of grazing intensity and the interactions with soils may have obscured or accentuated the effects of weather.

The greater plant populations of big sagebrush under the heavy stocking rate on the upland soils generally confirm the observations of other investigators, but are opposed to those of Reed and Peterson (in press). However, their study was conducted during a period of generally higher precipitation and recovery from the drought of the mid-1930's.

The greater population of big sagebrush on the terrace soils under the light stocking rate at the end of the study points out effects of soil (and site) differences and the differences in interaction of soils with grazing.

The favorable effect of light as compared with heavy grazing on plant numbers of silver sagebrush could be deduced from knowledge of its higher palatability. However, previous work indicated that utilization of this species was usually slight on summer-use cattle range.

The lower proportion of big sagebrush plants in crown class I under light stocking on the upland soils is probably a reflection of increased competition from the more vigorous and varied herbaceous plant cover there, despite probably inhibitory effects on big sagebrush establishment and growth of increased trampling and soil compaction which occurred under the heavy stocking rate. It is believed that differential utilization of the sagebrush plants is not an important factor here. The lack of differences in the proportions of big sagebrush plants in crown class I between stocking rates on the terrace soils indicates that one or a combination of characteristics of these soils are major factors influencing plant establishment. They are apparently more important in this respect than any differences in plant cover, competition, and possible soil compaction due to the differential grazing.

The almost continuous decrease in the proportions of big sagebrush in crown classes I and II and the parallel increase in crown class III on both soils under both stocking rates seems more related to weather than to other factors.

Plant numbers of silver sagebrush under heavy grazing were low throughout the study (Table II). In this circumstance a change in the crown class (or height class) distribution of a few plants has a large influence on proportions. For this reason the comparisons of proportions of this species were viewed conservatively.

The greater proportion of silver sagebrush plants in crown class I under light stocking on both soils is largely due to differential grazing pressure. The resprouting ability of this species would seem to operate to overcome this effect of differential grazing, but apparently was not able to do so. The increase in this crown class on the upland soils under heavy stocking in 1957 and 1959 above the proportions under the light stocking, paralleling the increase on the terrace soils under light stocking, is probably due to differential soil and site influences.

The greater proportion of silver sagebrush plants in crown Class III under light stocking

on both soil groups during the early part of the period and the similarity of proportions under both stocking rates on both soils during the latter part seems to indicate some delayed interaction of weather and grazing. It appears that during the drier early part of the study light stocking favored this crown class, but that during the more moist latter part grazing had essentially no effect. This is a logical deduction from the knowledge that grazing is usually more detrimental to drought-weakened plants. The rapid decrease in crown Class III on the terrace soils between 1957 and 1959 while the proportions in this class remained fairly constant on the upland soils indicates a weather-soil interaction, the mechanics of which are not readily evident.

The uniform and continuous decrease in the proportion of smaller big sagebrush plants with time and a corresponding increase in the larger plants may indicate progressive age of the stands. Blaisdell (1949) found that an established grass stand is highly competitive with young sagebrush plants. It may be that a good seed year for this species had occurred shortly before initiation of this study, but that some combination of the herbaceous cover on the sites, weather, and possibly grazing prevented subsequent establishment of seedling stands.

The lack of uniform variation in height classes of silver sagebrush with time may be partly explained by low number of plants. While a slight tendency for such a trend is evident there is considerable variability in height classes from year to year. Perhaps silver sagebrush seedlings are not as susceptible to competition or the resprouting and suckering ability of this species aids establishment of young stands despite variations in weather or grazing. There is little doubt that the greater proportion of taller silver sagebrush plants under the light grazing on both soils is due to the grazing factor.

The distinct trend for a smaller proportion of big sagebrush plants under 10 cm high and more of the larger plants under light stocking on the upland soils, and the remarkable similarity in height classes under both stocking rates on the terrace soils (except in 1957) clearly indicate an interaction of soils and grazing. It appears that light grazing causes a reduction in the younger age classes and an increase in the older age classes on the upland soils, but has little effect on height classes on the terrace soils. Probably the main mechanisms operating here under light stocking on the upland soils are increased plant competition for the young plants from the more vigorous grass stand under light stocking,

and increased trampling and breakage of the large plants under heavy grazing.

The parallel effects of stocking rate differences on height-class distribution of silver sagebrush on both soils are due to differential use of the species. These trends are not as distinct for silver as for big sagebrush perhaps indicating that trampling, soil compaction, and plant competition affect the species differentially, or that the resprouting ability of this species partly offsets the effects of browsing. If the latter be true then it follows that livestock utilization of silver sagebrush on this summer-use range has been greater than previously recognized.

Several broad differences exist between the upland and terrace soils which no doubt account for much of the differences in plant populations, growth characteristics, and reactions to grazing pressure of the two sagebrush species on the soils. The upland soils are more favorable to plant growth. They are generally deeper, of lighter texture, and have higher infiltration capacity. One of the terrace soils, Beckton silty clay, is saline in the surface layers with many small areas of slick spots. These have low infiltration and are practically devoid of vegetation. Surface crusts are present on two of the terrace soils. At present it is not possible to more precisely correlate the differential plant responses on the two soil groups with differences in any one or combination of these soil characteristics.

SUMMARY

A study was initiated in 1949, near Miles City, Montana, to observe the effects of heavy and light grazing and soil differences on the number and growth characteristics of big and silver sagebrush (*Artemisia tridentata* and *A. cana*).

Thirty plots each 10 x 12 m were established on 3 of the 5 major soil groups present and on both heavily and lightly stocked range areas. Plots were sampled in 1949, 1955, 1957, and 1959.

The areas were grazed from May 15 to late October. The climate, topography, soils, and vegetation of the study area are typical of a large portion of the Northern Great Plains.

On the heavily grazed areas stocking rates averaged 1.85 acres/A.U.M. and on the lightly grazed ones 3.33 acres.

Both growing season and annual precipitation averaged only 86% of the long-time means.

Results of the study indicate the following:

1. Number of plants per acre of big sagebrush was influenced as much by soil differences as by stocking rates.

2. Heavy grazing favored greater numbers of big sagebrush plants on upland soils, but on terrace soils stocking rate had no effect.

3. Light stocking consistently favored higher numbers of silver sagebrush on both upland and terrace soils.

4. Greater proportions of seedlings of big sagebrush and fewer mature plants (on basis of crown diameter) were present under heavy stocking than under light on the upland soils, but stocking rate had little effect on crown-class distribution on the terrace soils.

5. Higher proportions of seedlings and mature plants of silver sagebrush (on basis of crown diameter) were present on both upland and terrace soils under light stocking than under heavy during the early part of the study period. During the latter part the effects of stocking rate largely disappeared.

6. A continuous decrease in the proportion of shorter big sagebrush plants and an increase in the taller plants were observed under both stocking rates on both soil groups throughout the study.

7. Smaller proportions of the shorter big sagebrush plants and greater proportions of the taller plants were present under light grazing than under heavy on upland soils, but there was little or no effect of stocking rates on height class distribution on terrace soils.

8. A trend was evident for a smaller proportion of the shorter silver sagebrush plants on the upland soils and a greater proportion of large plants on both soils under light stocking than under heavy stocking.

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AN INVESTIGATION OF THE ECOLOGY OF *MERTENSIA CILIATA* IN COLORADO

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Mertensia ciliata (James) G. Don, an herbaceous perennial in the Boraginaceae, is the most common tall *Mertensia* of the western United States. The mountain environments in which it occurs impose strict conditions to which all stages of its life cycle must be adapted. This is a study of the ecological life history of *M. ciliata* to determine how adaptation to this special environment is exhibited by the species. The identification of the factors limiting survival and reproduction of the plant in at least one area was a second objective. The field work was performed near the Rocky Mountain Biological Laboratory (subsequently referred to as the R.M.B.L.), 9 miles north of Crested Butte at an elevation of 9500 ft (2900 m) in Gunnison County, Colorado (Fig. 1).

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SYSTEMATICS

Williams (1937), and more recently Popov (1953), have revised part or all of the genus *Mertensia*, which includes 45 species in the North Temperate Zone according to Popov. The 23 species recognized for North America by Williams are mainly in the western United States, the heaviest concentration in western Colorado where this study was made. Williams recognizes 3 varieties of *Mertensia ciliata*, in addition to the typical variety *ciliata* which is the subject of this paper and will be referred to simply as *M. ciliata*. The names and distributions of these varieties are in Figure 1. Several other species occurring sympatrically with *M. ciliata* were near the R.M.B.L. but no case of natural hybridization of *M. ciliata* with any of these other species was observed. Cronquist, however, has observed a natural hybrid between *M. ciliata* and *M. alpina* (Torr.) G. Don in Montana (p. 222 in Hitchcock *et al.* 1959). An attempt to artificially cross *M. ciliata* with *M. fusiformis* Greene (119, 120)¹ in their undisturbed habitats near the

¹ Figures in parentheses following binomials here and subsequently are collection numbers for voucher specimens, one set of which generally has been deposited in the University of Utah herbarium and a duplicate set retained by the author. Vouchers for the populations of *M. ciliata* studied in this work have the numbers: 113, 114, 115, 116, 117, 118, and 224.

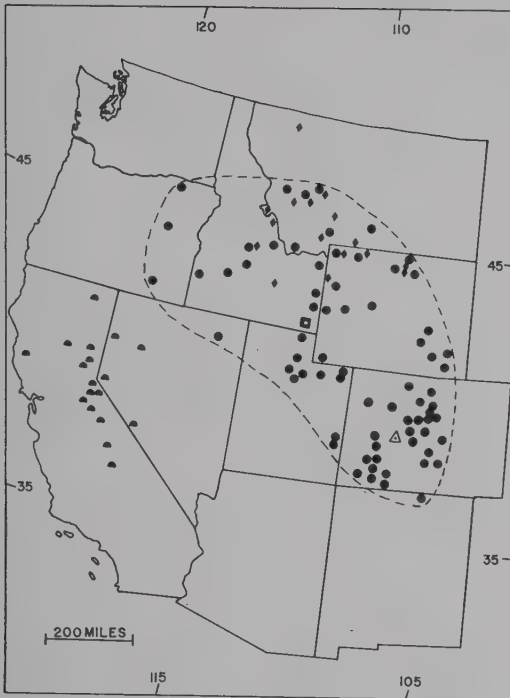


FIG. 1. Natural distribution of *M. ciliata* and its subspecies. ● = *M. ciliata* (James) G. Don (typical); ♦ = *M. ciliata* v. *subpubescens* (Rydb.) Macbr. & Payson; ■ = *M. ciliata* v. *stomatoides* (Kellogg) Jepson; ▲ = *M. ciliata* v. *latiloba* Williams (known only from the type locality in southeastern Idaho); △ = location of the Rocky Mountain Biological Laboratory. Data are based upon specimens cited in Williams (1937). Each dot represents one to many county records, a total of 225 specimens being represented by the map. The dotted line outlines the range of *M. ciliata* v. *ciliata*, upon which this study was made.

R.M.B.L. failed to yield viable seeds. A study of inter- and intra-clonal variability of *M. ciliata* in this locality by Jeanette Pelton (1959) demonstrated considerable somatic and genetic variability in the floral organs within a narrowly circumscribed area. A conspicuous variation occasionally observed in this region was pink flower color, instead of the normal blue of mature flowers (flower buds are normally pink in either type). Most of the pink-flowered plants were growing in the same soil adjacent to normal individuals suggesting genetically rather than environmentally induced change.

The species gradually decreases in height with increasing elevation, but whether this represents an ecocline in stature is not known. Clements and his associates (Clements 1929; Clements, Martin, and Long 1950) claim to have "con-

verted" *M. ciliata* (under the name of *M. sibirica* Don, an Asian species from which *M. ciliata* is now usually segregated) into 4 other species during transplant experiments in Colorado. There is no evidence, however, for the heritability of these changes, suggesting that these "conversions" resulted from the considerable somatic plasticity of *M. ciliata* grown in widely different environments producing phenocopies of the other species.

Britton (1951) found all the *Mertensia* species studied up to that time had a diploid chromosome number of 24 except for a single population of *M. ciliata* (collected near Boulder, Colorado) which was a tetraploid with 48. Some general hypotheses regarding migrations and evolutionary relationships within the genus *Mertensia* are presented by Holm (1927), Williams (1937), Lawrence (1937), Popov (1953), and Cooper (1936), in addition to those by Clements *et al.* (1950).

The population size of *M. ciliata* in the study area appears large because of the abundance and gregarious habit of the species. The actual breeding population size is much smaller, however, since vegetative reproduction results in large clones of many individuals. Nevertheless, genetic drift is probably not a significant factor at this time in most of the study area. The total population of clones is still large, and the breeding population is not much reduced by either autogamy or apomixis. The flowering season of individual clones is relatively prolonged, thereby promoting overlap in breeding seasons, but the clones are probably very long-lived. Effective geographic isolation is mostly lacking in the area in spite of the rugged topography. The colonies often occur nearly continuously along streams from low to high elevations, and some of the pollination vectors are probably strong fliers or readily blown by high winds.

M. ciliata is one of the more ornamental species in the genus, and is recommended for rock gardens (Bailey 1928). Most authors suggest "bluebells" as a colloquial name for the genus *Mertensia*, and Kelsey and Dayton (1942) recommend "mountain bluebells" as the standardized vernacular name of *M. ciliata*. Several other names, however, are in the literature.

OCCURRENCE

Range

The geographic range of *M. ciliata* and its varieties is shown in Figure 1. Williams (1937) considers this to be the most common and widely distributed of the tall aestival species of *Mertensia* within the Rocky Mountains. One specimen al-

legedly collected in Arizona but lacking a definite locality is omitted from the figure.

Although the species is probably most common in the "subalpine" or "Canadian" zone in Colorado (approximately 9000 ft (2740 m) to 11,500 ft (3500 m)), in that state alone it extends at its lower altitudinal limit to the plains at 5500 ft (1680 m), and at its upper limit to above timberline at 13,000 ft (3960 m) (Harrington 1954). In the Front Range of Colorado it has been described as primarily but not exclusively a "montane zone" species (Clements 1920), but Weber (1953) prefers to call the species "subalpine" there also.

Climature

Long-term weather records from the weather bureau station nearest the R.M.B.L. are in Figure 2. Because of differences in elevation, rugged topography, and distance (9 miles) of this station (Crested Butte) from the localities where the species was studied in detail, the data only suggest the microclimates in the study areas. For this reason, during the summer of 1954 temperature and precipitation data were collected at 5 contrasting sites where *M. ciliata* was abundantly represented within a distance of 7 miles from the R.M.B.L. Bimetallic maximum-minimum thermometers placed on the ground under reflective ventilated metal shelters, and totalizing rain gauges, were utilized close to clumps of *M. ciliata* in the habitats described in the legend to Figure 3.

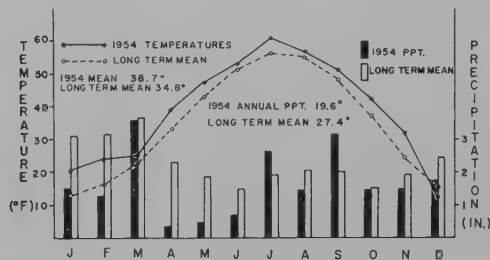


FIG. 2. Temperature and precipitation data for Crested Butte (elevation 8855 ft or 2700 m) during 1954 in comparison with long term means (U. S. Dept. Commerce 1955). The absolute long-term temperature extremes for this station are -42°F (-41.1°C) and 91°F (32.8°C).

The data of Figure 2 indicate that the temperatures during 1954 averaged somewhat higher but the precipitation of July and August averaged about the same as the long-term means. With the exception of the highest station (#4), results indicate that the net precipitation of July and August reaching the ground through the vegeta-

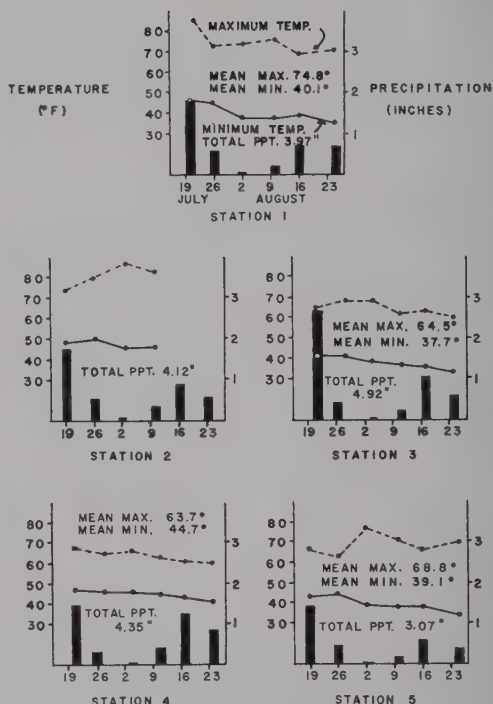


FIG. 3. Temperature and precipitation for the summer of 1954 in 5 microhabitats near the R.M.B.L. Station 1: 9700 ft (2960 m); *Salix* shrub-meadow vegetation; thermometer in shade of shrubs, rain gauge fully exposed. Station 2: 9800 ft (2990 m); instruments under moderately dense aspen forest; thermometer destroyed by cattle about August 11. Station 3: 9900 ft (3020 m), within dense spruce-fir forest. Station 4: 10,800 ft (3260 m), under moderately dense spruce-fir canopy. Station 5: 9600 ft (2960 m), in mixed aspen-conifer forest of medium canopy.

tion canopy increased with increasing altitude (Fig. 3). The effects of topography and vegetation in modifying an altitudinal temperature gradient are especially clear: mean minimum temperatures at the highest station (#4) were considerably higher than those at stations even as much as 1200 ft (366 m) lower, although mean maximum temperatures were lower at the highest localities. Although frost may occur any time during the summer, 1954 was warmer than average and frost was not recorded at any of the 5 stations, even where the thermometer was fully exposed. The data of Figures 2 and 3, being limited in both time and space, give an incomplete idea of the climatic tolerances of the species as a whole, but they show that the area has short growing seasons, cool summer temperatures, moderate summer precipitation, and extreme

winter temperatures. Prolonged and heavy snow cover is another significant feature not indicated in the figures. An extreme continentality and short growing season seems to be characteristic of all the area in which the species occurs naturally (Fig. 1), although often to a lesser extreme than in the study area. The growing season of *M. ciliata* probably greatly exceeds the "frost-free" season, although the actual degree of freezing tolerated by actively vegetative or flowering plants is not known. Climatic data from *M. ciliata* habitats in the Frost Range of Colorado (Clements, Martin, and Long 1950, Whitfield 1933) are basically similar to the data above.

M. ciliata may be considered a near-sciophyte, since it thrives and fruits normally at 10-20% of full sunlight. Clements (1920) lists *M. ciliata* (under the name of *M. sibirica*) as an "indicator" of deep shade in the Front Range montane zone. In this study, however, the species was found often enough in open meadows or exposed at the edges of willow clumps to preclude considering it a shade "indicator," although it probably occurs more frequently in shaded or semi-shaded habitats in the area. Since the plant thrives and fruits well in full sun in many moist sites, it is not obligatorily sciophytic.

Topography

The topographic situations occupied by *M. ciliata* near the R.M.B.L. were usually above average in moisture supply. A characteristic situation is along permanent streams (Fig. 4), but the species may occur wherever the water table, seepage, or intermittent drainage channels provide relatively constant moisture during the growing season. Near the upper limits of its altitudinal range the need for such moist sites is not so conspicuous; there the species occurs on open hillslopes or talus where late snow-melt is doubtless a compensating moisture factor. However, not all wet soil areas in the area are suited to the species; it rarely occurs on the most poorly aerated sites. The species does frequently grow along lakeshores, but even here it is most abundant along the better aerated stream inlet areas.

Other observers have noted this preference for rather moist situations throughout the range of *M. ciliata* (Abrams 1951, Ashton 1933, Clements 1929, Cox 1933, Davis 1952, Harrington 1954, Harshberger 1911, Hitchcock *et al.* 1959, Holch *et al.* 1941, Langenheim 1953, Peck 1941, Pesman 1946, Weber 1953, Williams 1937). Of the specimens of *M. ciliata* var. *ciliata* from 8 states cited by Williams which bear habitat data, 111 (75.5%) were collected from "river bottoms,"

"creek banks," "headwaters," "damp lakeshores," "swampy ground," and similar distinctly wet situations. Twenty eight (19%) occurred in slightly less wet areas, such as "moist hillside," "moist meadows," "moist ravines," "moist ground in shade," and "moist ledges." Only 8 specimens (5.5%) occurred in sites which might be interpreted as dry, as "dry stony slopes" or "cliffs" (10,000 ft [3048 m] in Wyoming); "limestone cliffs" (9800 ft [2990 m] in Wyoming); "rolling plains (6000 ft [1830 m] in Wyoming); "rocky dry creek bank," "alpine rock slides," and "rocky roadside" (Wyoming, altitudes not given); and "loose rock crevices" (11,800 ft [3600 m] in Utah). Even such apparently dry situations may have underground seepage or snow accumulation, or be at elevations or latitudes which partly compensate for a drier topographic situation. Near the study area, on the other hand, the writer observed one clump of *M. ciliata* in full sun in a dry shallow gully at 9000 ft (2740 m). Williams has observed the plant on "open hillsides which soon became dry," and Graham (1937) in "dry meadows" at subalpine and alpine elevations in the Uinta Mountains, Utah. However, clones of *M. ciliata*, because of their active vegetative reproduction, are probably very long-lived and thus, once established, may persist in a site which subsequently becomes drier owing to physiographic, climatic, or vegetational changes.

Soil

Soil pits were dug and samples obtained from the microclimate stations and numerous other sites to investigate the range of soil conditions tolerated by *M. ciliata* in the study area. There was no correlation of the distribution of the species with parent material. Vigorous stands grew on parent materials of glacial till, raw igneous talus, disintegrating shale, river alluvium, beaver dams, and decaying logs. McCullough (1948) in a nearby conifer forest found *M. ciliata* abundant on fallen logs which were so decayed that their outlines were indefinite.

Table I presents data from certain sites where the species grew and nearby wet-soil stations where it was absent. These particular stations were selected for comparison because the only consistent and evident differentiating factor was the slightly higher water table in the soils from which the species was absent, although *M. ciliata* characteristically grows on moist to wet soils. Where water flow is rapid, the species tolerates nearly saturated soils, but even where it grows along stream banks the soil surface is usually several inches above the water. The lack of cor-

relation of the occurrence of *M. ciliata* with other possibly significant soil factors (Table I) seems to support this interpretation. Thus, textural variations have little effect; the preponderance of fine-textured soils is probably mostly due to the scarcity of coarse-textured soils nearby, although many of the soils sampled were rocky. Organic matter and base exchange capacity varied erratically, and the means of the stations with and without the species were not significantly different at the 5% level. The per cent base saturation averaged high, and the pH was slightly acid to circumneutral, but these values showed no statistically significant difference between the stations with and without the species. Cox (1933) reports a much more acid soil (pH 5.4) in alpine meadows in which she recorded *M. ciliata*. Probably some measurement of oxidation-reduction potentials in undisturbed wet soils would show definite correlations with the distribution of the species. Soils which smelled strongly anaerobic, in fact, did not support the plant.

Associates

In a quantitative analysis of the vegetation of a large area adjacent to the R.M.B.L., Langenheimer (1953) lists *M. ciliata* as an important herbaceous component (with 75% frequency) in a study of 32 spruce-fir stands, where it was especially common along stream banks. She also lists *M. ciliata* as an important member of the *Veratrum* societies and general streamside vegetation of the region. It was not a common plant of the "wet meadow"

or "snowflush" sites. My observations tend to support these data.

Only species growing in identical soil adjacent to clumps of *M. ciliata* should be regarded as having soil tolerance ranges which overlap those of this species. The following list includes some of the more frequently associated vascular plants observed by the writer closer than one foot to a colony. The communities and species listed pertain primarily to the altitudinal range of the microclimate stations (Fig. 3) near the R.M.B.L. Spruce-Fir (*Picea-Abies*) Forest (Fig. 4): *Abies lasiocarpa* (Hook.) Nutt.; *Cardamine cordifolia* Gray (207); *Epilobium adenocaulon* Hauskn. (217); *Luzula parviflora* Desv. (215); *Osmorrhiza obtusa* Fernald (212); *Oxypolis fendleri* Heller (210); *Picea engelmanni* (Parry) Engelm.; *Polemonium delicatum* Rydb. (213); *Saxifraga arguta* D. Don (216); *Senecio triangularis* Hook. (206); *Stellaria umbellata* Turcz. (214); *Vaccinium* spp.

Aspen (*Populus*) Forest: *Elymus glaucus* Buckl. (221); *Epilobium adenocaulon*; *Fragaria ovalis* (Lehm.) Rydb.; *Geranium richardsonii* Fisch. & Trautv. (211); *Heracleum lanatum* Michx. (208); *Ligusticum porteri* Coult. & Rose (222); *Oxypolis fendleri*; *Populus tremuloides* Michx.; *Taraxacum officinale* Wiggers (111); *Thalictrum fendleri* Engelm. (205).

Willow (*Salix*)-Meadow Vegetation: *Achillea lanulosa* Nutt. (219); *Aconitum columbianum* Nutt. (209); *Agropyrum trachycaulon* (Link)

TABLE I. A comparison of certain soil characteristics at 7 representative sites where *M. ciliata* is present and at 7 nearby wet-soil sites from which it is absent

	Station	TEXTURE ¹				% Organic Matter ³	Base Exchange Capacity ⁴ (m.e./100g)	% Base Saturation ⁴	pH ⁵
		% sand 2-.05mm	% silt .05-.002mm	% clay 0-.002mm	Class name ²				
<i>M. ciliata</i> present	A	26.6	51.2	22.2	silt loam	8.7	19.7	95.2	6.3
	B	26.2	52.4	21.4	silt loam	14.0	26.5	99.6	6.8
	C	27.3	47.6	25.1	loam	8.9	20.5	94.1	6.6
	D	—	—	—	organic	57.1	41.3	91.5	6.8
	E	—	—	—	organic	38.5	47.5	98.1	6.4
	F	28.0	42.5	29.5	clay loam	6.4	15.3	85.6	6.6
	G	—	—	—	organic	51.5	60.6	90.1	6.5
	Mean	—	—	—	—	26.44	33.05	93.46	6.57
<i>M. ciliata</i> absent	H	—	—	—	organic	38.9	43.0	73.7	6.5
	I	38.0	41.5	20.5	loam	10.7	19.9	91.6	5.9
	J	28.2	46.6	25.2	loam	17.1	28.9	93.8	6.3
	K	25.0	41.7	33.0	loam	13.2	23.8	87.8	6.3
	L	32.1	50.5	17.4	silt loam	9.4	8.9	100.0	7.6
	M	34.3	43.8	21.9	loam	7.4	16.0	99.2	6.6
	N	44.8	29.4	25.8	loam	11.1	22.4	91.5	6.5
	Mean	—	—	—	—	15.40	23.27	91.08	6.53

¹ Hydrometer method (Bouyoucos 1951).

² Soil Survey Staff (1951).

³ Walkley-Black chromic acid method (Jackson 1958).

⁴ Determined by leaching with ammonium acetate and titration (Russell and Stanford 1954).

⁵ Glass electrode pH meter determinations.



FIG. 4. Habitat view near Station 3 in spruce-fir forest opening. *M. ciliata* is the dominant herbaceous plant along the stream banks.

Malte (223); *Delphinium barbeyi* Huth. (220); *Epilobium adenocaulon*; *Geranium richardsonii*; *Heracleum lanatum*; *Hydrophyllum fendleri* (Gray) Heller (203); *Ligusticum porteri*; *Poa pratensis* (218); *Salix drummondiana* Barrett v. *subcoerulea* (Piper) Ball; *S. barclayi* Anderss.; *Saxifraga arguta*; *Taraxacum officinale*; *Thalictrum fendleri*; *Veratrum californicum* Durand.

Of these 3 communities, *M. ciliata* is least frequent in the aspen forest, where it is often restricted to streamlets or ravines. In those aspen stands which have resulted from recent burning of conifer forest, the species is probably most commonly a pre-fire relic. The willow-meadow vegetation, in which *M. ciliata* occurs as frequently as in spruce-fir forest, is particularly heterogeneous, varying from essentially pure *Salix* to strictly herbaceous vegetation sometimes dominated by *Veratrum*. Both streamside and open moist (but usually not wet) meadow habitats are represented. The meadow and aspen communities are strongly influenced by moderate to heavy late season grazing by cattle. This has

favorable such plants as *Taraxacum* and *Veratrum*, but it is not clear whether the frequency of *M. ciliata* has been significantly affected. In addition to these 3 communities, the species is common in the region under spruce-fir krummholz at timberline; less frequent above timberline in willow-herb vegetation, and has been noted rarely among sagebrush (*Artemisia tridentata* Nutt.) in rocky ravines at its lower altitudinal limit.

In Wyoming, *M. ciliata* (typical) occurs in spruce-fir forests (Oosting and Reed 1952) and moist sites in "xeric grasslands" within the spruce-fir zone (Hanna 1934, Graham 1937). It is a common pioneer species in mesic alpine meadows in Utah (Hayward 1952), and is present in the yellow pine, aspen, and spruce belts in Utah and Nevada (Graham 1937, Tidestrom 1925). Elsewhere in Colorado, *M. ciliata* has been reported in wet meadow communities at 11,000 ft (3350 m) by Cox (1933), in the "Canyon Forest Formation" (*Populus angustifolia* James, *Alnus tenuifolia* Nutt., etc.) of the low foothills of north-central Colorado (Harshberger 1911), and as a conspicuous element among the undergrowth in subalpine forests of *Picea engelmanni*, *Pinus aristata*, *Pinus flexilis*, and *Populus tremuloides* in the Front Range (Whitfield 1933).

Although *M. ciliata* is usually found in damp sites, it was not observed in adjacent but somewhat more saturated soils supporting *Pedicularis groenlandica* Retz., *Carex aquatilis* Wahl., or *Juncus saximontanus* A. Nels. Even though the soil tolerances of these 3 species at least locally do not appreciably overlap those of *M. ciliata*, this is not true of several of the wet-soil species listed as associates above. For example, *Epilobium adenocaulon* frequently grows with *Juncus saximontanus* and is also a common associate of *M. ciliata*.

None of the species in the above lists is a constant associate of *M. ciliata* or is closely similar to it in ecological requirements even within the limited area of this study. This fact, in conjunction with the local occurrence of *M. ciliata* in communities varying widely in composition and physiognomy, suggests that the distribution of the species is distinctly "individualistic."

LIFE HISTORY

Flowering

M. ciliata bears its flowers on axillary peduncles each bearing moderately dense clusters of ebracteate cymes (Figs. 5 and 6). Figure 7 shows approximate flowering and fruiting phenology at the microclimate stations together with temperature records. The lack of relationship

between advancement of flowering and the 3 temperature data in the figure may be explained partly by the records beginning too late in the season, after anthesis had begun. Also, earliest dates of uncovering by snow and soil temperatures are probably significant. Using adequate data and refined techniques, Lindsey and Newman (1956) found close correlation of temperature with flowering for *M. virginica* (L.) Link. in Indiana. Abundant soil moisture is essential for flowering and the relatively dry site at Station 5 permitted only a short season of flowering and fruiting. Where moisture is abundant, as at Station 4, or after heavy rains, additional cycles of buds are initiated and the flowering season is significantly prolonged. The latest seasons during the course of this investigation were 1955 and 1957, in which *M. ciliata* first began blooming (near Station 5) on July 2 and 6, respectively.



FIG. 5. A single stem of *M. ciliata* showing habit of foliage, shoot, and inflorescence.

The anthokinetic cycle (Fig. 8) agrees in general with that illustrated for *M. sibirica* (= *ciliata*) by Clements and Long (1923). Contrary, however, to their illustrations made in the Front



FIG. 6. Closeup of part of the inflorescence from Figure 5 showing simultaneous development of buds, flowers, and young fruits. The corolla on the left is distorted as a result of parasitism by bud mites.

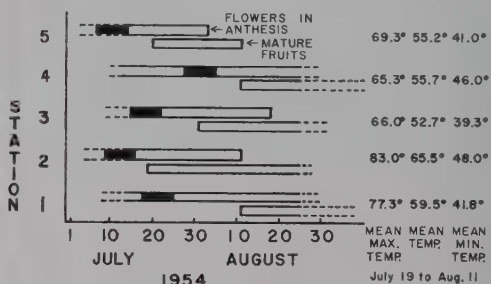


FIG. 7. Phenology at the microclimate stations of Figure 3 and temperature records through August 11 (when instruments were destroyed at Station 2). The solid portion of the upper bar at each station represents the approximate week of maximal flowering. The dotted portions are suggestive extrapolations before and after the study.

Range of Colorado, in this study the stigma did not protrude from a still unopened corolla, and the style seemed to bend little if at all after anthesis. Mature corollas are normally blue but the buds are pink, and the usual presence of both open flowers and buds in the same inflorescence increases the color contrast (Kerner 1895). The open flowers emit a mild fragrance, and a clear sweet nectar develops at the base of the corolla. The sequence of development in one series of observations (Fig. 8) in a shady site required about 10 days from stage 1 to 4 (pollen shedding), and 4 more days to stage 6 where the corolla has fallen. Very commonly, the corolla is not ab-

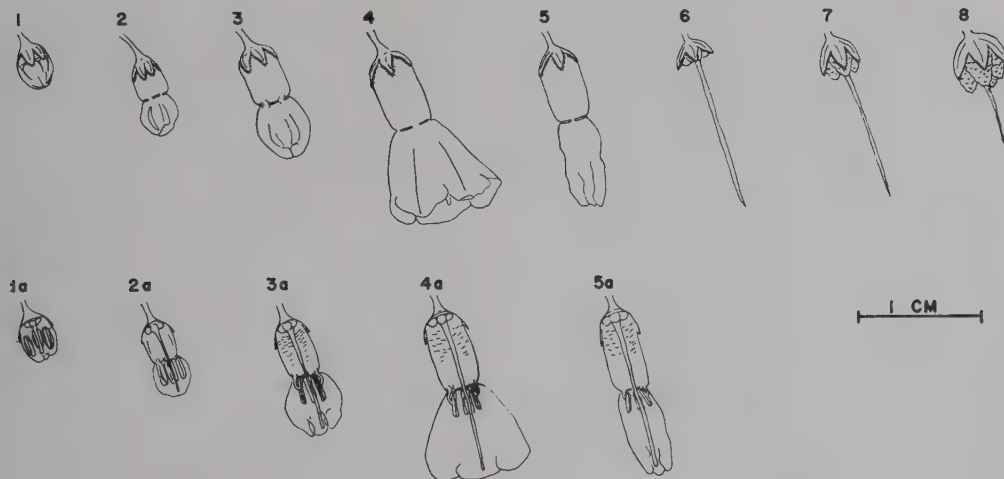


FIG. 8. Flower bud formation, anthesis, and fruit maturation in *M. ciliata*. In the plant shown, the sequence from 1 to 8 required 35 days.

scissed and dries in place, but the fruit often develops normally nevertheless.

The style is usually slightly inserted within the open corolla, and has a nearly capitate and moderately sticky stigma. The latter becomes receptive before the anthers dehisce and remains so for some time after the corolla with its empty anthers has fallen. Unlike certain species of the genus, *M. ciliata* is not heterostylous.

The 5 anthers are versatile, introrse, and longitudinally dehiscent. They usually open in the morning within a few hours after the corolla lobes spread (stage 4, Fig. 8). The pollen is usually gone by late afternoon, although up to 2 days may elapse before it is shed during inclement weather. Tests in moist chambers showed that 100% humidity causes closure of anthers which still retain pollen, although they remain open outdoors on cloudy days. The anthers are difficult to wet, and this, in conjunction with the pendant habit of the open flower, affords considerable protection from the rain to the pollen and nectar.

An experiment designed to test the possibility of autogamy was performed by bagging 175 flower buds on a single clone. These were divided into 3 groups, one being cross-pollinated with fresh pollen from a clone 3 miles away, the second self-pollinated with pollen from the same flower or another flower in the same bagged inflorescence, and the third group being left bagged but untouched. The pollinations were repeated on several successive days, and the bags were not permanently removed until the corollas had fallen and the stigmas had withered. The results were

$18.7 \pm 5.1\%$ fruit set and matured from cross-pollination, $16.1 \pm 4.9\%$ from self-pollination, and zero from the unpollinated group. The difference between the cross- and self-pollinated groups is not statistically significant, but the absence of fruit set from the unpollinated flowers precludes autogamy or apomixis, at least under the experimental conditions.

Pollination can be effected by several types of insects. In a freshly opened flower the 5 anthers are appressed along their lines of dehiscence so they almost completely close the corolla tube, the wide filaments and yellowish puberulent projections (fornices) adding to the obstruction. Moderate pressure is required to force the anthers aside, but if this is done an opening 1.5-2.0 mm is available. Only insects of minute size (which would not ordinarily effect pollination) or those with a proboscis at least 9 mm long can readily reach the nectar at the base of the tube. The pollen itself is sticky, and clings to any object it touches.

The following insects were among the more common visitors observed during July:

HYMENOPTERA

Apidae: *Apis mellifera* L., *Bombus melanopygus* Nyl., *B. mixtus* Cr., *Psithyrus insularis* (Sm.).

Colletidae: *Colletes p. paniscus* Vier.

Megachilidae: *Osmia* spp.

DIPTERA

Bombyliidae: *Systoechus oreas* O.S.

Muscidae: *Hylemya* sp., *Paregle* spp.

Flies of the family Muscidae were frequent visitors of *M. ciliata* but probably relatively ineffectual as pollinators since they usually failed to enter the corolla tube. Apidae (bumble and honey bees) were common visitors and are important pollinators, but the bee-fly *Systoechus* came only rarely. Clements and Long (1923) found a different group of floral visitors for *M. pratensis* Heller in the Front Range of Colorado.

The role of the small bees, *Colletes* and *Osmia*, is difficult to evaluate. They were the most common Hymenopteran visitors, and they frequently entered the corollas and probably effected pollination. More commonly they apparently cut a hole at the base of the corolla and stole the nectar without pollinating. Counts of several hundred corollas at 20 localities in the area in 2 different years ranged from zero to $98.1 \pm 1.4\%$ with holes. Plants at over half the localities observed, especially those in the sun where these bees are most active, showed high proportions of pierced flowers. Fruit frequently sets from such flowers, since the ovary is uninjured, and various insects visit these flowers from the mouth of the corolla. Other insects, such as the Muscidae flies, also visit the holes although it is doubtful that they cut them.

In addition to the above insects, a minute beetle (Staphylinidae) is an almost constant inhabitant of flowers and may be an occasional agent of self-pollination. The beetles only occasionally fly to other flowers, but even then rarely leave the same clone. They probably rarely touch the stigma, so it is unlikely that they are effective in cross-pollination.

In general, insect visits were not frequent, except in plants exposed to the sun on non-windy days. Since the species commonly occurs also in shady sites, pollination failure might help explain the relatively poor fruiting found in many localities during the study.

Defective pollen also contributes to the frequently poor fruit set. The anthers may appear partly or entirely brown and shriveled before anthesis, and a high proportion of the resulting pollen grains are shrunken or fail to take acetocarmine stain. A count of pollen grains from defective anthers gave $83.5 \pm 2.5\%$ defective, whereas abnormal pollen constituted only $12.9 \pm 2.7\%$ of normal-appearing anthers. Within a single inflorescence, both normal and abnormal flowers are found, but the condition is more frequent in some clumps than in others. Both genetic and environmental factors may be involved, but the relative role of these is not clear. In 1959, 13 out of 20 stations near the R.M.B.L.

had plants with at least some defective anthers. Normal fruits occasionally develop from flowers with all anthers defective, indicating normal megasporogenesis. Blackened and shriveled ovaries were also observed, both on plants with normal and with defective anthers, although this condition was less common than flowers with abnormal anthers but normal-appearing ovaries.

A more significant cause of poor fruit production is probably insect and mite injury to the flowers. Particularly important were a minute bud mite (Eriophyidae: *Aceria* sp.) feeding on the ovary, anthers, and corolla within the flower bud which consequently remains pink or becomes pale and dry before anthesis; and an unidentified diptera larva feeding on anthers, corolla, and ovary within the unopened buds. These two parasites varied in their relative importance in different years. In 1954 the mite was present at most stations and serious at several of them, the diptera larva being infrequent at this time, whereas in 1959 the situation was almost reversed.

A few other insects, such as aphids (Aphidoidea), were sometimes observed feeding on flowers, but none was abundant except very locally. A mildew fungus (*Erysiphe cichoracearum* DC.), which attacks mainly the vegetative parts, also can deform buds, flowers, and young fruits where it is particularly severe. At certain stations (such as microclimate Stations 1 and 5) drought seemed to be an important cause of lack of fruit set. Under these conditions many of the buds would dry and usually become pale or brown without opening, often simulating injury by the bud mite.

Fruiting

The fruit of *Mertensia ciliata* is a group of 1 to 4 readily-separating rugose nutlets (Figs. 8 & 9). The fruit in Figure 8, in a cool shady location, required 3 wks to mature from stage 6 to stage 8, but the process is quicker in warmer situations.

Measurements of nutlets selected randomly from a large collection from several adjacent colonies gave an average maximum length of $3.46 \pm .05$ mm and an average maximum width of $2.30 \pm .05$ mm. The average fresh weight of over 100 filled nutlets from this same sample, determined 6 wks after maturity and exposure to the normally high temperatures and humidity of late summer in Indiana, was 0.00299 g/nutlet. The moisture content of these nutlets at this time was 8.1%. This weight is greater than the 0.001675 g given for *Mertensia maritima* Don. by Porsild in Salisbury (1942), but the shingle habitat of the latter species is more open than those of *M. ciliata*. The weight of *M. maritima* is close

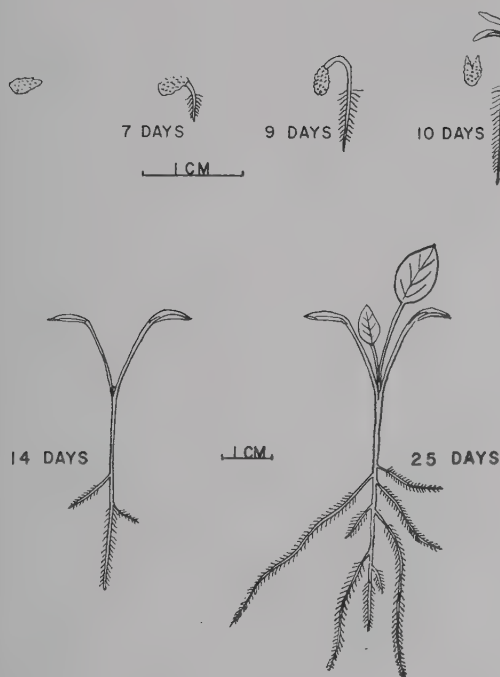


FIG. 9. Germination and early seedling stages of *M. ciliata* grown in sand in the greenhouse.

to that given by Salisbury as the mean seed weight of species of open habitats in the British Islands, while that of *M. ciliata* lies between the mean seed weights of species of closed but non-shady and of semi-shady sites. Except that *M. ciliata* is also found in deep shade, where seed weights tend to average higher, these figures correlate well with the respective habitats of these two species of *Mertensia*.

Production of sound seed was rarely high; it was difficult to find colonies where seed could be conveniently collected in quantity. Frequently no viable nutlets matured in a colony, even though flowers were abundant. Probably because of drought and increased insect and mite attacks at lower altitudes, production was usually greater at the higher elevations, within the altitudinal limits of the microclimate stations. Moderate shade had little effect upon fruiting. At Station 4, where fruit production was above average, fruit counts of 41 flowering stems showed no statistically significant difference (as the 5% level) between stems in full sun, in partial shade equivalent to 40-60% of full sun, and in shade equal to 10-20% of full sun. The average production of these stems combined was 24.4 ± 2.5 nutlets, which is the "average seed output" per flowering stem (Salisbury 1942).

All the potential nutlets in a flower do not usually develop in a given fruit. Of the total number of fruits counted in the above study, $11.4 \pm 1.5\%$ bore 4 nutlets, $21.7 \pm 1.9\%$ bore 3 nutlets, $39.4 \pm 2.3\%$ had 2 nutlets, and $27.5 \pm 2.1\%$ one nutlet. These figures are based only on nutlets which appear normal, although cutting tests of 880 nutlets from several stations showed $28.4 \pm 1.5\%$ (samples ranging from 6.7%-45.8%) had shrunken embryos or none at all. If we take as the per cent viability the number of filled seeds (71.6%), the product of this figure with that of the average seed output is 17.5, or the "average reproductive capacity" per flowering stem. The "average reproductive weight," 0.052 g, is given by the product of the average reproductive capacity and the average weight of the filled seeds.

In comparison with the many perennial herbaceous species of even shaded habitats studied by Salisbury (1942), all the above values for *M. ciliata* would rate low, but the figures for this species are derived from an inadequate sample. The cool temperatures and short growing season may contribute to a low seed productivity. The even lower fruit production (zero in many colonies) found elsewhere in the area in several successive years can be explained by several apparently unrelated factors. Drought, floral parasites, defective pollen, and pollination failures have been suggested. Mildew and foliage-eating insects have been observed on immature fruits, but these are more important in lowering fruit production indirectly through their effects on the foliage. Pine siskins, *Spinus pinus pinus* (Wilson) feed upon the nearly mature fruits (H. Levi, personal communication). The year 1956 was especially poor for fruit production for undetermined reasons. In apparently similar habitats some clumps may fruit well while adjacent ones fruit poorly, suggesting genetic variability is also involved. Because of effective vegetative methods of reproduction and a resultant probably indefinite life-span, the immediate dependence upon seed reproduction by the species is greatly reduced, and a poorly-fruited clone might long persist and even spread locally by rhizome growth and transport by floods.

Dispersal

The main dispersal unit in *M. ciliata* is the individual nutlet, 1 to 4 of which develop from each ovary. Rhizome fragments are doubtless also important in local downslope movements during floods.

The nutlets mature from mid-summer to early fall in the area. The period during which mature and shedding fruits were present at each of the microclimate stations studied in 1954 is in Figure 7. The fully mature nutlets are usually dark brown to blackish. Abscission of the nutlets frequently begins while they are still green or greenish-yellow, just before the color changes, but many are retained until fully darkened. All the nutlets within a given fruit are not necessarily released simultaneously, and empty or shrunken nutlets usually do not abscise readily.

No special dispersal mechanisms are evident in *M. ciliata*, and there are probably several dispersal agents. The nutlets are somewhat roughened (Figs. 8 and 9) and might occasionally adhere to the fur of mammals. Their external roughness, their light weight (only 0.00299 g) and their height above ground (often over one meter) would favor the nutlets being blown short distances by strong winds. Pine siskins perhaps sometimes disseminate the seeds. Since the species characteristically occurs along streams and drainage channels, downslope dispersal of both nutlets and rhizome fragments by high waters must be significant, particularly since this would place the seeds in a suitably moist habitat. Plants from rhizomes which were evidently buried by alluvium during floods have been observed in the area. Upslope dispersal probably depends on wind, mammals, and birds. The generalized nature of the dispersal adaptations in *M. ciliata* contrasts with the specialized seed-dissemination adaptations of the strand-inhabiting *M. maritima* (Ridley 1930).

Germination

M. ciliata possesses a moderate to high degree of inherent seed dormancy, although not as complete as that of *M. fusiformis* (Pelton 1956). A series of germination tests and pre-treatments were made from 1953 to 1956 under a variety of conditions to study the dormancy mechanism of *M. ciliata*. Seeds were collected from several stations during August of each of these 4 yrs. The fruiting clusters were dried in the sun one day and then shaken in a paper bag to gently release the ripe seeds. These were separated from flower parts by sieving. Since the unripe nutlets are retained strongly on the gynobase of the receptacle, only ripe seeds which were naturally dehiscing were obtained and used by this technique.

Repeated germination tests of several hundred seeds placed between moist filter paper in Petri dish germinators immediately after extraction

gave negative results. Tests were carried out under the fluctuating temperature conditions (5–22° C) prevailing during normal August weather in the natural habitat of the species. During examinations the nutlets were exposed to light in these and subsequent tests, but for the remaining time they were in the dark.

This deep dormancy of freshly-harvested seeds could be largely overcome by several kinds of pre-treatments. Some dormancy was lost during open room-temperature storage for several months at Butler University in Indiana. Germination tests at a constant 18° C averaged $22.5 \pm 5.4\%$ "real germination" (per cent of filled seeds which germinated as determined by terminal cutting tests) after such storage. Great variability among different collections was evident, however.

Cold-moist stratification of seeds between moist filter papers at 5° C for up to 346 days resulted in only $6.7 \pm 1.4\%$ real germination when subsequently transferred to 18° C (some seeds germinate at the 5° C temperature). Seeds stratified for 200 days at 5° C in pots of moist and well-aerated soil obtained from beneath a colony of *M. ciliata* and subsequently placed at 18° C yielded no germination. Neither of these results differed significantly from the untreated controls.

The most effective treatments breaking seed dormancy of the species were those which partly or completely removed the seed coats. Hot water treatment was ineffective, but soaking in concentrated sulfuric acid yielded an average of $76.8 \pm 2.2\%$ real germination at 18° C, peak germination being reached 12 days following the treatment. The untreated controls for this test, which had been under dry room-temperature storage for several months, gave $34.1 \pm 4.2\%$ germination.

Shaving one corner of the seed coats with a razor resulted in $52.3 \pm 10.9\%$ real germination, in contrast to $2.2 \pm 1.8\%$ for the untreated controls. Removing the thick outer nutlet coat completely and leaving the thin inner coat uninjured gave negative results. Breaking or removing the inner coat after removal of the outer coat yielded an average of $90.0 \pm 3.4\%$ real germination in several tests, in contrast to the average of $17.0 \pm 2.1\%$ germination of the controls.

This suggests that impermeable (or conceivably mechanically restrictive) nutlet coats, specifically the thin inner coat, are primarily responsible for the dormancy of *M. ciliata* seeds. Under natural conditions fungal attack breaking down the seed coats, alternate wetting and drying or freezing and thawing, or abrasion in washing along stream channels would permit germination

to occur. In one test of the effectiveness of fungal and bacterial activity, however, a 3 month period at 18° C in moist and well-aerated native-habitat soil, followed by 4 months at 5° C, was insufficient for fungal activity to permit germination of a majority of the seeds. It is possible that for many seeds 2 yrs in the soil is required to break dormancy in the cool climate where *M. ciliata* grows. No germination was obtained in one test of seeds planted in pots of soil sunken in the ground and left to overwinter in a natural habitat at the R.M.B.L.

Germination is epigeous, and the cotyledons expand and become photosynthetic (Fig. 9). Endosperm is lacking. The seeds germinate at 5° C, but a better response is obtained at 18° C after the seed coat dormancy has been removed. Germination under natural conditions probably occurs mostly or entirely in the spring from seeds which have been in the soil for at least the fall and winter and perhaps for 2 or more years. The normal June drought in the region (Fig. 2), however, significantly decreases the survival chances of spring-germinating seedlings in all but the moistest sites. Only 2 naturally-germinated seedlings were observed in the field during the study. These had apparently germinated in the spring, and were still in the cotyledon stage in early July. Both seedlings disappeared by midsummer for undetermined reasons. It is probable that seedling survival frequently depends on new bare areas created by high waters along the drainage channels which the species frequents, and by the extensive rodent activity characteristic of open meadows in the region. In mature conifer forest frequent colonization of partly decayed logs demonstrates that seedlings do not depend entirely on newly-bared mineral soil, however. Compared to multiplication by rhizomes reproduction by seeds is probably rare. As with many other rhizomatous species, seed reproduction in *M. ciliata* apparently functions mainly in dispersal and in permitting gene recombination by cross pollination, but rhizome reproduction is responsible for most local multiplication and spread.

Growth

The shoots of *M. ciliata* (Fig. 5) expose considerable surface in comparison with the dry matter involved, since the leaves are large and thin, the stems usually hollow (or nearly absent in vegetative rosette shoots), and the amount of woody tissue in the aerial parts negligible. Although the elongate stems do not droop appreciably (except at the tips) when the leaves are wilted, in dense colonies the shoots can become

so etiolated and weak that rain and wind result in a centrifugal lodging outward from the center of the clump. Williams (1937) reports stems of this species reach 120 cm. This is 13 cm above the maximum height observed in the study area, and considerably above the average of flower-bearing stems. At timberline shoots reached a maximum height of 92 cm in the area. In years of near-normal spring precipitation, flowering stems were rarely observed below 30 cm, but they occasionally reached only 18 cm following the exceptionally dry spring of 1960, and Williams (1937) reports them to 10 cm. Vegetative rosettes derived from rhizomes extend down to almost seedling size.

The thin mesomorphic leaves are extremely subject to temporary wilting, drooping conspicuously, often with their margins curled downward and inward until they touch. Plants in full sun regularly wilt during most of the day, even following a rain when the sun emerges or in sites where the soil is moist. In dry situations, the leaves frequently become reddish-green or reddish-yellow by late August. The lower leaves may die and shrivel by midsummer in relatively dry habitats, but leaf abscission does not occur.

Whitfield (1933) has reported and illustrated the ecological anatomy of *M. ciliata* (= *sibirica*) leaves in the Front Range of Colorado. He finds their internal structure is typically mesomorphic, with a single palisade layer, loose spongy tissue, and no hypodermis. Leaves on plants at 12,300 ft (3750 m) were slightly more xeromorphic than those at 8335 ft (2540 m), with a somewhat thicker palisade layer, less intercellular space, and thicker epidermal walls at the high altitude. Unlike certain other *Mertensia* species he examined, Whitfield found *M. ciliata* lacked stomata on the upper leaf surface at all altitudes. Clements *et al.* (1950), working in the same area, found the stomata were much more abundant on the lower surface, but occurred on both sides of the leaf in some shoots presumably of this same species. My observations of a number of plants agree with those of Whitfield.

Transpiration studies in which *M. ciliata* was used for phytometers were undertaken both by Whitfield (1933) and by Clements *et al.* (1950). Results indicate this species behaves essentially like the other mesophytes used by these investigators. Osmotic measurements of sap expressed from the leaves of *M. ciliata* by Clements *et al.* ranged from 7.1 atm in the shade at 8000 ft (2440 m) to 14.1 atm in full sun at the same elevation. Although these are representative values for mesophytic herbs of cool temperate

climates in general, the basic adaptations of the species to the special habitats in which it occurs are doubtless mainly physiological rather than strictly morphological.

Following the initial spring and early summer surge of growth, shoot development essentially ceases with the onset of flower bud formation. New elongate sucker shoots often develop sporadically later in the summer, but except in the wetter sites ordinarily only after heavy rains.

Cattle graze *M. ciliata*, but it is apparently less palatable than many of its associates. Usually only the elongated shoots and inflorescences are eaten, the basal leaves and rosette sprouts being left. The plant remains very common along stream flats which are relatively heavily grazed, and it is quite possible that moderate cattle grazing tends to favor the species over some of its competitors. Its vegetative spread and apparently long-lived habit could readily explain the plant's persistence under even heavy grazing.

The most serious fungus found attacking the shoots in the region was a conspicuous whitish mildew, named under "Flowering." This parasite was most common in moist shaded habitats, but also occurred in full sun. Growth and fruiting of *M. ciliata* were only occasionally much affected by this or other fungus in the years of this study. The rust fungus, *Puccinia mertensiae* Peck, has been reported on *M. ciliata* by Arthur (1934) and is listed by Seymour (1929), but was not found by the writer.

Insect attacks of the vegetative parts were only occasionally limiting to growth or fruiting during the study. A leaf spot condition, believed by Dr. G. B. Cummins to represent the sites of insect punctures, was of minor significance. Aphids and leaf mining larvae were infrequently observed, except in 1959 when aphids were relatively important at a few stations. The most active foliage feeder in the locality, especially abundant in 1957, was the larval stage of the pericopid moth, *Gnophaela latipennis vermiculata* G. & R., which locally caused severe reduction of growth and fruiting.

The majority of the perennating buds of *M. ciliata* are on the enlarged basal caudex or "crown" just beneath the soil surface, rather than on the elongate rhizomes. Consequently, the species is best classified as a scapose hemicryptophyte (Braun-Blanquet 1932). In 1959, by July 2 the buds on the crown were purplish, about 5 mm long, and lacked woody scales. The enlarged crown occurs where the original rhizome becomes vertical, close to the soil surface, and numerous buds result in a horizontal expansion within a few

years just beneath the ground level. After many years, or perhaps decades, such crowns become very large: one averaged 12 x 15 cm in horizontal spread and was 7 cm thick. Numerous thickened and intertangled rhizomes and stem bases compose such an old crown, part of which may be decayed or "pithy" and part hard and woody. Erect shoots arise each year from the perennating buds on the crown and ordinary rhizomes radiate outward from it in all directions. Many fine and large roots develop from the crown and from the adjacent normal rhizomes.

Counts of root hairs on one plant suggest that these are sparse. This may be related to the wet habitat in which the plant grows. No evidence of mycorrhiza was obtained. Root branching was not particularly profuse; some current season roots were unbranched for several centimeters, although others were relatively well branched.

Holch *et al.* (1941) have described and illustrated an excavated *M. ciliata* root system, which they apparently consider to be a tap-rooted species lacking rhizomes. This observation disagrees with mine and that of taxonomic descriptions as well (e.g., Williams 1937). All the stems excavated in this study were attached to rhizomes or to crowns formed from rhizomes. In a few cases in deep soil the rhizome was nearly vertical, and might easily be mistaken for a tap root. Externally, older rhizomes which have lost their scale leaves and have formed thick bark are similar to roots. The pith of the rhizome resembles the stele of the root in coloration, and observation with a hand lens is often necessary to make the distinction.

Vegetative Reproduction

The gregarious, colony-forming habit of *M. ciliata* results from active rhizome growth. Large colonies can eventually become subdivided into several portions by death of the inter-connecting rhizomes, and rhizome fragments may serve as a local means of dissemination. Road graders and bulldozers break up the rhizomes and distribute them along the roadsides. Probably almost all the plants in these man-disturbed areas are of rhizome rather than seedling origin.

Current season rhizomes have scale leaves about 1 cm long. Adventitious roots can develop the same season as that in which the rhizome develops, but only from scale leaf axils. Sometimes roots do not develop immediately from the newly formed rhizome, but possibly do in a subsequent year. Rhizomes ranged from 1.2 mm in diameter to over 10 mm. Annual rings were indistinct. The oldest rhizome in which the rings

were distinguishable had 9 growth layers and was 6 mm in diameter.

There was considerable variation in depth of rhizomes. At microclimate Station 3 in dense forest most of the rhizomes were only 12 mm deep in the duff, or A₀ horizon. Near Station 1 in willow vegetation the rhizomes averaged about 25 mm deep in fine alluvial soil, although some were 50 mm below the ground. Rhizomes which are nearly vertical for at least a portion of their length frequently occur.

Hundreds of young rosette plants were excavated in several habitats. All were attached to rhizomes, although in many cases the rhizome was decayed close to the shoot. Probably even the latter rosettes were derived from rhizomes which subsequently decayed rather than from seedlings. Rosettes vary from 1.2 cm in height with a single leaf to 25 cm high or higher with up to about 6 leaves but no visible stem. The rhizomes giving rise directly to the small rosettes were also usually small, but in several instances these often nearly vertical rhizomes were attached to a deeper and usually comparatively large more or less horizontal rhizome. Multiplication by rhizomes appears to be the only important method of local reproduction and spread, although the occupation of more distant localities presumably must normally be initiated by seedlings.

The density of rhizome-produced rosettes within a clump of *M. ciliata* can be quite high. A square meter plot established in the center of a colony of about average density in full sun on fine alluvium near microclimate Station 1 gave the following results: 3 flowering stems over 30 cm tall; 0 non-flowering stems over 30 cm tall; 5 vegetative but elongate stems less than 30 cm tall; and 63 rosettes, lacking elongate stems. A similar plot at Station 4 on residual loam soil in an exceptionally dense colony in part shade gave the respective values of 28, 84, 42, and 69.

All stages of the life cycle of any successful species must be at least minimally well adapted, but the superior efficiency of one stage probably can partly compensate for the less perfect adjustment of other stages. The local abundance of *M. ciliata* is probably a result of the great efficiency of its rhizomatous habit, since multiplication by seeds does not appear more effective than that of many less common species.

SUMMARY

Mertensia ciliata (James) G. Don is a widespread herbaceous perennial (hemicryptophyte) of the Boraginaceae occurring primarily in the Rocky Mountains, but represented by a sub-

species in the Sierra Nevada. The species is common to locally abundant in deeply shaded spruce-fir forest to fully exposed meadows, and from the foothills to above timberline. It is adapted to climates of extreme continentality, cool summers, and short growing seasons. It usually frequents moist to wet habitats, at least in the study area (Gunnison County, Colorado) but is excluded from the most poorly aerated soils. It tolerates mineral or organic substrata of diverse origins. Pollination of the blue pendant flowers is effected by a number of insect types, including Hymenoptera and Diptera. Autogamy and apomixis apparently are absent, and cross-pollination is not obligatory. A moderate proportion of the plants produce some defective pollen; this and pollination failure, direct injury by parasites, suppression by drought, and other factors contribute to a frequently low seed reproductive capacity in the study area. The main dispersal unit is the roughened nutlet, from 1 to 4 of which are produced by each ovary, but these are not specialized for transport by a single agent. Seed viability is moderate, but germination is significantly delayed by an apparently impermeable inner seed coat. Although seedlings are rare in the study area, and most reproduction is vegetative, seeds are responsible for most dispersal and for gene recombination by cross pollination. The thin leaves are typically mesomorphic, and are occasionally seriously parasitized by fungi or severely eaten by insects or livestock. The species is strongly rhizomatous, and tends to form long-lived clonal aggregations. Rhizomes provide the primary method of local multiplication and contribute to downstream dissemination during floods and distribution along roads by grading operations. The efficiency of the rhizomatous multiplication of this species tends to compensate for the less effective reproduction by seeds and is largely responsible for its local abundance.

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VEGETATION AS A SOIL-FORMING FACTOR ON THE QUILLAYUTE PHYSIOGRAPHIC UNIT IN WESTERN CLALLAM COUNTY, WASHINGTON¹

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Several treeless areas (i.e., prairies) in an otherwise heavily forested locale are known in Clallam County, on the Olympic Peninsula in northwestern Washington (Wheating 1936, Fowler and Wheating 1941). These persistent elements of the landscape, in a region where the climate is extremely favorable for the growth of the surrounding forest, provide an opportunity to compare influences of prairie and forest vegetation upon the development of soil properties.

The site of this study was the Quillayute Prairie and the immediately adjacent forested area in western Clallam County. Locally the soils of both prairie and forest have developed from the same deep sediments of silty texture. These soils lie within a terrain that exhibits a topographic unity suggestive of a single physiographic unit. Evident dissimilarities of soil morphology within this physiographic unit appear to be attributable largely to the influence of vegetation as a soil-forming factor.

This work was done to provide some clarification of soil genesis as it is affected by vegetation, and to provide data for categorizing a local soil.

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DESCRIPTION OF THE AREA

The Quillayute physiographic unit occupies a narrow belt within the interfluvium formed by the Dickey River and Colby Creek on the northwest, and the Sol Duc River on the southeast (Fig. 1). The area has a gentle westerly slope, and lies between 120 and 300 ft (37 and 91 m) above sea level. The southern boundary of the physiographic unit is coincident with the southern boundary of the Quillayute Prairie; it is formed by an escarpment that drops abruptly to a recent terrace of the Sol Duc River, 60 to 80 ft (18 to 24 m) below the prairie. The northern boundary

of the physiographic unit lies somewhat beyond the prairie, but its position was not mapped. The northern boundary of the prairie is marked by an abrupt change from low-growing herbaceous plants to dense forest, but it is without topographic discontinuity.

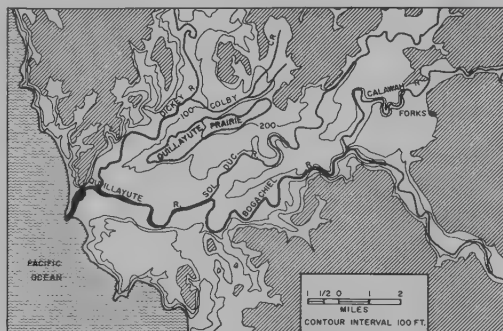


FIG. 1. The Quillayute physiographic unit is a narrow strip of ground whose southern boundary is an escarpment. This boundary is coincident with that of the Quillayute Prairie. The northern boundary of the physiographic unit was not mapped; it lies slightly beyond the northern boundary of the prairie, but is not marked by topographic discontinuity. Except for the prairie, all land areas below 300 ft elevation appear without pattern on the map. The figure was drawn from the 1938 LaPush and Forks sheets of a 1:62500 army tactical map, contour interval 20 ft, Corps of Engineers.

Since vegetation appears to be the principal variable in soil formation within the Quillayute physiographic unit, it was studied more intensively than were the other factors. *Tsuga heterophylla* and *Picea sitchensis* are the prominent members of the forest community; the physiognomy of the prairie is determined, in large degree, by the fern *Pteridium aquilinum* var. *pubescens*. There is no evidence that trees have ever grown on the main portions of the Quillayute Prairie.

The soil of the Quillayute Prairie, Quillayute silty clay loam, was described by Wheating (1936), who cited the lack of charcoal as evidence that the prairie proper has never been forested. A subsequent paper by Fowler and Wheating (1941) described the soil organic matter of this and related soils in Clallam County

¹ Scientific Paper No. 1938 Washington Agricultural Experiment Stations, Pullman. Work was conducted under Project 1168.

but did not discuss a possible origin of any of the prairies. Smith *et al.* (1951) also described the Quillayute soil and suggested that fires set to provide open areas for hunting may have formed the prairie, but they did not explain the lack of charcoal.

The A₁ soil horizons of the prairie are characterized by a high organic matter content and a very dark gray to black color. The A₁ horizons of the immediately adjacent forested soil contain quantities of organic matter comparable with those found within the prairie solums, but are yellowish brown to reddish brown. Internal drainage of soils under both prairie and forest vegetation is good; the profiles show no evidence of gleying.

METHODS OF ANALYSIS

The western end of the Quillayute physiographic unit was selected for intensive study. There the vegetation and soil appeared to be least disturbed, and several strips of clearly non-climax forest could be examined for the effect of forest succession on soil properties (Fig. 2). The low-growing vegetation of the prairie and forest was analyzed by estimation (using no aiding device) of species coverage along transects running parallel to the ecotone. The transects were located near sites 1 and 2 (Fig. 2); each transect consisted of a series of fifty contiguous 2- x 5-dm plots. Two series for each community were analyzed; one was adjacent to the ecotone, and one was about 120 m within the representa-

tive vegetation. Each 2- x 5-dm plot was considered as a unit of 100%, and the cover of each species occurring in a plot was estimated on this basis. Coverage for each species within a transect (Table I) was obtained by conversion of these individual plot values to a total (50 plots) basis. Frequency was determined on the basis of rooted shoots. Data on sociability were not taken.

Mosses and liverworts collected in representative forest and prairie plots were identified by H. S. Conard, Lake Hamilton, Florida. Jones (1936), Abrams (1923-1960), and Hitchcock *et al.* (1955) were the authorities used for nomenclature of vascular species. Life forms (Table I) are presented according to the system of Raunkiaer (1934).

Soil profiles were described, bulk density cores were obtained, and samples for laboratory analysis were collected from pit walls. The samples for analysis were passed through a 2-mm sieve, except for an occasional discarded pebble. In addition, two transects across the ecotone were studied, using auger samples collected at points where the vegetation changed.

Particle-size analysis was by the method of Kilmer and Alexander (1949), except that material first retained by the 300-mesh sieve was repeatedly triturated with a rubber pestle to disrupt plate-like aggregates not dispersed by shaking; however, trituration was not completely effective. Exchange capacity was determined by an ammonium acetate method in which cations are replaced with ammonium at pH 7.0; this replacement, particularly of aluminum, was effected with difficulty, and probably incompletely. The absorbed ammonium was distilled off, using the phosphate buffer suggested by Shrikhande (1941). Exchangeable sodium and potassium were determined using the Beckman Model DU flame spectrophotometer, modified by using acetylene as the fuel, a Perkin-Elmer burner, and an air atomizer; otherwise the method was essentially that of Bower *et al.* (1952).

Soil reaction was determined on a soil-water paste with a glass electrode-equipped pH meter. Total carbon was determined by a wet combustion procedure (Smith and Weldon 1940). Nitrogen was determined by a Kjeldahl procedure, using copper sulfate and selenium powder as the catalyst. Oxidizable material was estimated by the procedure of Walkley (1946) except that the titration of excess dichromate was with an automatic titrator. Active carbon was estimated by the procedure of Moodie (1950). Mineral grains of the very fine sand separate were divided

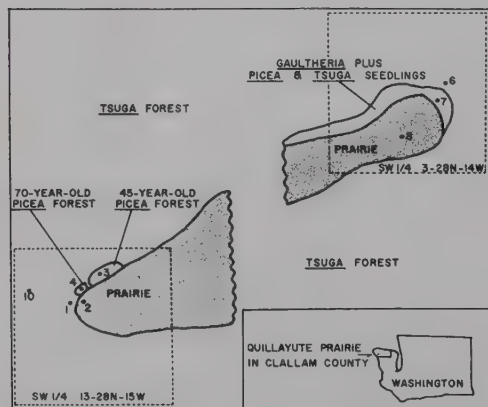


FIG. 2. Sketch map of the two ends of the Quillayute Prairie, showing sampling locations and vegetational units. Disagreement among available base maps makes the legal descriptions somewhat uncertain. Locations with respect to 1953 vegetational boundaries are more accurate. Site 9, not shown, was about 800 m west of site 4.

TABLE I. Coverage, frequency and life form of vascular plant species found in climax forest understory, prairie, forest-ecotone and prairie-ecotone. Results based upon analysis of fifty 2- x 5-dm plots for each of the 4 study areas.

Life forms: Th—Therophyte; G—Geophyte; H—Hemicyrptophyte; Ch—Chamaephyte; P—Phanerophyte

Species Exhibiting Greatest Frequency and (or) Coverage Values in		% COVERAGE (Cov.) AND % FREQUENCY (Freq.) OF VASCULAR PLANTS IN								Life Form
		Forest		Forest-Ecotone		Prairie-Ecotone		Prairie		
		Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	
Forest										
<i>Oxalis oregana</i>	16.4	58	—	—	—	—	—	—	H	
<i>Polystichum munitum</i>	44.9	70	4.0	22	—	—	—	—	G	
<i>Tsuga heterophylla</i> (seedling) ¹	0.3	10	0.1	2	—	—	—	—	P	
<i>Vaccinium parvifolium</i>	2.6	6	1.4	6	—	—	—	—	P	
Ecotone										
* <i>Agrostis alba</i>	—	—	—	—	1.8	8	—	—	G	
<i>Athyrium filix-femina</i>	0.8	2	—	—	32.8	72	—	—	G	
<i>Blechnum spicant</i>	1.4	8	0.7	6	3.3	8	—	—	G	
<i>Bromus vulgaris</i>	—	—	—	—	0.4	4	—	—	H	
<i>Cystopteris fragilis</i>	0.1	2	0.2	8	0.1	2	—	—	G	
* <i>Daucus carota</i>	—	—	—	—	2.4	16	—	—	H	
<i>Disporum smithii</i>	0.3	2	0.7	8	4.1	38	—	—	G	
<i>Galium aparine</i>	—	—	—	—	1.4	6	—	—	Th	
<i>Galium triflorum</i>	—	—	—	—	6.9	52	—	—	H	
<i>Gaultheria shallon</i>	—	—	13.8	64	11.8	30	—	—	P	
<i>Maianthemum dilatatum</i>	0.4	6	2.3	30	9.3	70	1.3	22	H	
* <i>Poa pratensis</i>	—	—	—	—	0.4	4	—	—	G	
<i>Polemonium carneum</i>	—	—	—	—	0.7	6	—	—	H	
* <i>Prunella vulgaris</i>	—	—	—	—	0.4	6	—	—	H	
<i>Rhamnus purshiana</i>	—	—	0.1	2	3.3	6	—	—	P	
<i>Rubus parviflorus</i>	—	—	—	—	35.7	78	—	—	P	
<i>Rubus spectabilis</i>	—	—	0.1	2	—	—	—	—	Ch	
<i>Smilacina liliacea</i>	—	—	—	—	0.9	6	0.3	2	H	
<i>Symphoricarpos albus</i> var. <i>laevigatus</i>	—	—	—	—	9.7	34	—	—	P	
<i>Tellima grandiflora</i>	—	—	—	—	10.6	62	—	—	H	
<i>Tiarella trifoliata</i>	—	—	—	—	0.4	4	—	—	H	
<i>Viola adunca</i>	—	—	—	—	0.3	2	—	—	H	
Prairie										
<i>Achillea millefolium</i> (possibly <i>A. m.</i> var. <i>californica</i> , or * <i>A. m.</i> var. <i>millefolium</i>).....	—	—	—	—	7.2	38	23.1	80	G	
<i>Agrostis oregonensis</i>	—	—	—	—	0.4	4	2.1	14	H	
<i>Anaphalis margaritacea</i>	—	—	—	—	3.8	16	9.6	38	G	
* <i>Anthoxanthum odoratum</i>	—	—	—	—	3.3	16	14.1	58	H	
<i>Aquilegia formosa</i>	—	—	—	—	—	—	0.7	6	H	
<i>Camassia quamash</i>	—	—	—	—	—	—	0.5	8	G	
* <i>Cerastium viscosum</i>	—	—	—	—	—	—	0.1	2	Th	
* <i>Chrysanthemum leucanthemum</i>	—	—	—	—	0.4	4	1.7	16	H	
* <i>Cirsium arvense</i>	—	—	—	—	—	—	1.3	12	G	
<i>Eriophyllum lanatum</i>	—	—	—	—	—	—	12.5	58	Ch	
<i>Fragaria bracteata</i>	—	—	—	—	2.1	24	5.7	58	H	
<i>Galium boreale</i>	—	—	—	—	3.4	26	7.9	54	H	
* <i>Holcus lanatus</i>	—	—	—	—	8.2	48	30.2	82	H	
* <i>Hypericum perforatum</i>	—	—	—	—	—	—	20.2	88	H	
* <i>Hypochoeris radicata</i>	—	—	—	—	—	—	4.1	26	H	
<i>Luzula parviflora</i>	—	—	—	—	0.3	2	0.4	4	H	
<i>Malus fusca</i>	—	—	—	—	0.3	2	8.6	16	P	
* <i>Phleum pratense</i>	—	—	—	—	—	—	0.8	10	H	
<i>Prunella vulgaris</i> subsp. <i>lanceolata</i> ..	—	—	—	—	—	—	10.6	36	H	
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	—	—	0.4	4	64.5	98	81.6	100	G	
<i>Ranunculus occidentalis</i>	—	—	—	—	—	—	0.3	10	H	
<i>Rosa</i> sp.?.....	—	—	—	—	0.7	6	0.7	18	P	
<i>Sisyrinchium idahoense</i>	—	—	—	—	—	—	0.8	10	H	
<i>Solidago canadensis</i> var. <i>salebrosa</i> ..	—	—	—	—	—	—	4.5	26	G	
<i>Spiraea menziesii</i>	—	—	—	—	16.9	52	15.9	62	P	
<i>Stachys ciliata</i>	—	—	—	—	2.8	22	3.4	36	H	
<i>Trientalis latifolia</i>	—	—	—	—	0.5	10	0.4	14	G	

¹ Less than 10 cm high.

* Exotic species.

into heavy and light fractions (Jeffries and Jackson 1949) and then identified under a petrographic microscope after removal of iron oxides by a procedure which is essentially that of Jeffries (1947).

Iron was determined colorimetrically with o-phenanthroline (Snell and Snell 1949). Mineralogy of the clay separates was determined on size-separated samples freed of organic matter by hydrogen peroxide and of oxidizable iron by reduction with sodium dithionite. Calcium-saturated and glycerated material on a glass slide was X-rayed using a Norelco wide range X-ray diffractometer with copper K- α radiation and a nickel filter. Montmorins were identified by a peak at about 18Å. Illite was identified by a first order peak at 10Å. A first order peak at 14Å was used to identify chlorite plus vermiculite. Distinction between these two was based on presumed collapse of the 14Å peak of vermiculite following heating of K-saturated samples to 400° C; if a 14Å peak persisted following heating of samples to 500° C, chlorite was assumed to be

present. Kaolinite could be present without being recognized in the X-ray work; however, selected DTA curves did not suggest kaolin.

VEGETATION

Forest

The climax forest surrounding the Quillayute Prairie has relatively few vascular species (Table I). The study of five 5- x 25-m plots laid out adjacent to the west end of the prairie indicated that *Tsuga heterophylla* is the dominant arborescent species in this stand, which is illustrated in Fig. 3. This tree forms nearly pure stands within the general study area, with some *Picea sitchensis* present as a seral species. Growth-ring analysis indicates that this latter species is an earlier invader of the habitat. This *Tsuga* forest is reproducing itself; all ages, from seedlings to mature trees, are present. Subordinate vegetation is composed chiefly of *Polystichum munitum* and *Oxalis oregana*. Plot study data are representative of the coverage and frequency of species



FIG. 3. *Tsuga* forest community showing *Tsuga heterophylla* as the dominant arborescent species, with an understory of *Oxalis oregana* and *Polystichum munitum*. *Vaccinium parvifolium* is present but not readily identifiable in this view.

comprising this *Polystichum munitum*-*Oxalis oregana* union.

As the ecotone between forest and prairie is approached from the forest side (forest-ecotone, Table I), the composition of the subordinate union changes somewhat with the introduction of *Gaultheria shallon*. This species appears to be present only in the ecotone (Figs. 4 and 5). There it is quite prominent, although not a member of either the forest or prairie community. Several species of small trees appear to be confined chiefly to the ecotone; among these are *Acer circinatum*, *Malus fusca*, *Rhamnus purshiana* and *Alnus oregana*. *Malus* and *Alnus* are also found within the climax communities, but not as prominent

members. Within the forest-ecotone, trunks of *Acer* and *Malus* lean strongly outward toward the prairie (Fig. 4).

Picea sitchensis (normally a seral tree in this region) has invaded the Quillayute Prairie in an area about 75 m northeast of the forest plot-study location (site Q-3, Fig. 2). This even-aged stand (40-50 yr old, Fig. 6) is growing vigorously on the dark-colored soil, and apparently became established on fields abandoned about 1900 by early settlers of the region. *Picea* does not appear to be reproducing itself, and the stand is devoid of the subordinate vegetation associated with the climax forest. Evidently there is a considerable time lag before successful encroachment by these characteristic forest understory species can occur. The former boundary of the Quillayute Prairie is a short distance to the west of this young *Picea* stand, and occurs within the near-climax forest. There are numerous senescent plants of *Malus* and *Acer* along this old ecotone, their trunks leaning toward the prairie 60 m away. Other ecotonal species, especially *Gaultheria shallon*, are also present at this boundary.



FIG. 4. Ecotone from the forest side showing the dominant *Tsuga heterophylla*, with lower branches all on the open side. Note especially *Acer circinatum*, leaning toward the prairie, and *Gaultheria shallon*, both of which are associated with the ecotone.



FIG. 5. Ecotone from the prairie side showing the dense growth composed of *Gaultheria shallon*, *Acer circinatum*, *Alnus oregana*, *Rhamnus purshiana* and *Malus fusca*. A few fronds of *Pteridium aquilinum* var. *pubescens* can be seen in the foreground.



FIG. 6. Forty-five year old *Picea sitchensis* forest (approximate age when photographed in 1953) that is growing vigorously on the soil developed under prairie vegetation. Note the many dead limbs and the complete absence of undergrowth.

A grove of older *Picea* was also studied. This area (site Q-4, Fig. 2) lies a short distance southwest of the 45-yr-old stand. This grove is situated just within the forest side of the older forest-prairie ecotone referred to previously, and evidently became established at about the same time the region was initially settled. Core samples taken in 1953 indicated that these trees were 70-80-yr-old. This stand will be referred to as the 70-yr-old *Picea* forest. Records of a land survey

made in 1879 state that settlers were living on the Quillayute Prairie; at about this time the *Picea* stand began its development.

Prairie

Prairie vegetation consists principally of herbaceous species with a few scattered shrubs and deciduous trees (Fig. 7). From a study of two series of 2- x 5-dm plots (50 plots in each series) laid out at the western end of the Quillayute Prairie, it is apparent that *Pteridium aquilinum* var. *pubescens* is the dominant prairie species (Table I). Other members of the community, such as *Achillea millefolium*, *Anthoxanthum odoratum*, *Eriophyllum lanatum*, *Fragaria bracteata*, *Hypericum perforatum* and *Spiraea menziesii* are abundant, but possess low coverage values because most of the plants are small.



FIG. 7. Prairie vegetation showing the nearly complete dominance in mid-summer of *Pteridium aquilinum* var. *pubescens*. The small trees scattered over the prairie are *Malus fusca* and *Rhamnus purshiana*.

Certain species appear to be characteristic inhabitants of the forest-prairie ecotone. For example, *Gaultheria shallon*, *Athyrium filix-femina*, *Disporum smithii*, *Rubus parviflorus* and *Tellima grandiflora* have high frequencies within this ecotone, yet are absent or rarely encountered in the series of prairie and forest plots. *Rhamnus purshiana* is found near the ecotone, but is not a prominent member of the typical prairie community. Prairie plots contained an abundance of *Hypericum perforatum* and *Eriophyllum lanatum*, neither of which was found adjacent to the forest (prairie-ecotone). Other species (e.g., *Aquilegia formosa*, *Camassia quamash* and *Ranunculus occidentalis*) not present in the prairie-ecotone plots also appear in the prairie, but much less often than either *Hypericum* or *Eriophyllum*.

Plants encountered in the prairie and ecotone plots which are also commonly found on disturbed sites in the region include *Hypericum* and *Hy-pochoeris* (both noxious weeds), as well as species of *Anaphalis*, *Anthoxanthum*, *Cerastium*, *Chrysanthemum*, *Cirsium*, *Daucus*, *Phleum*, and *Prunella*; most of these are also exotics (Table I). Placement in Table I of certain species is arbitrary. Thus *Blechnum* shows the same frequency in both forest and ecotone, but greater coverage in the ecotone; *Spiraea* and *Trientalis* have greater frequencies in the prairie, but greater coverage in the ecotone. The life form classification is not absolute, since it varies somewhat with geographic location.

Pteridium aquilinum var. *pubescens* dominates the prairie in midsummer; however, 28 additional species are present in at least one or more of the plots (Table I). If vegetational analyses were made in late May or early June, *Pteridium* would be less clearly dominant than the coverage data indicate. *Pteridium* fronds do not completely unroll until the latter part of June; prior to that time many species have already flowered and set seed, thus completing their essential life functions before *Pteridium* becomes a serious competitor. Dense shade is uncommon under fully expanded *Pteridium*, and inadequate illumination would not appear to be an important factor in the distribution of shorter species growing beneath this fern canopy.

The eastern end of the Quillayute Prairie has been radically disturbed by fire, grazing and mowing, and was not considered suitable for formal vegetational analysis. *Pteridium* is also dominant throughout this section, but shows diminished stature (1+ m) as compared with the more vigorous plants (2+ m) on the relatively undisturbed western end.

This eastern portion has been enlarged in recent years, as evidenced by a belt, 30-60 m wide, of *Gaultheria shallon* along the north and east borders. This belt contains numerous seedlings of *Picea sitchensis* and *Tsuga heterophylla*. Several large *Picea* snags were also observed well out into the prairie, in a hummocky area which could have resulted from the uprooting of trees.

Soil appearance provides additional evidence of relatively recent prairie expansion. In contrast to the western portion, the characteristic dark gray A₁ horizon of the soil of the prairie does not extend into the edge of the forest. Instead, the gray gives way to an A₁ horizon which is very dark reddish brown (both colors when moist) at some distance from the northern and eastern prairie-forest boundary. Considerable

quantities of charcoal in the surface soil, as well as the direction of prevailing winds (from the southwest), make it appear likely that fires have influenced the extension of this eastern section.

The moss and liverwort compositions of climax Tsuga forest and prairie (not tabulated) are quite different. Only *Eurhynchium oreganum* was collected from both communities. Three other species were collected from plots in the prairie: *Aulacomnium androgynum*, *Brachythecium albicans* and *B. albicans occidentale*. Six additional species were collected from plots under climax forest: *Mnium punctatum* (the same as *M. glabrescens* Kindb.), *Plagiothecium elegans*, *P. undulatum*, *Pseudisothecium stoloniferum*, *Rhytidia delphus loreus* and *Scapania bolanderi*.

Prairie-Forest Dynamics

From observations made during this investigation, these factors and events are postulated to account for the present vegetation-soil pattern.

Exposure to the atmosphere of the fine-textured sediments comprising the soil-forming material provided a primary bare area. When both fine- and coarse-textured substrates are exposed under a climate favorable for the growth of herbaceous and woody plants, the initial tendency is for the former to colonize the silts and clays, and for the latter to become established on sands and gravels. If certain herbaceous species were among the early invaders of an area of fine-textured material, they might form a sod which would be inimical to the invasion of the habitat by woody species, but not detrimental to continued colonization of various herbs. Possibly certain biological barriers (of an unknown nature) created by this herbaceous community prevented or retarded the invasion and establishment of woody species upon these fine-textured sediments.

Salinity, high water table and soil structure might also have been involved in the establishment of a relatively stable herbaceous community on these sediments. The suggested estuarine origin of the Quillayute physiographic unit (see following section) could have created conditions of high salinity and an elevated water table, which were initially unfavorable for the development of arborescent species. However, subsequent stream-cutting and elevation of the area, abundant precipitation to leach out the salts and improved structure and aeration of the solum through incorporation of organic matter could have modified the habitat sufficiently to permit the invasion of trees. Whatever the reasons for the origin of an herbaceous community, once firmly established it might successfully resist invasion by arborescent

species for a long time. The Quillayute Prairie, therefore, is interpreted as a relic community.

Other factors in addition to soil texture which might retard forest encroachment upon such an area include stream-cutting, fire, human disturbance and seed source. Although it was stated that stream-cutting might have enhanced the spread of trees, this factor could also have helped preserve the herbaceous community. Stream-cutting to the north and south by the Dickey River, Colby Creek and the Sol Duc River has partially isolated the prairie. It is possible that only within comparatively recent times has the forest invaded from younger and less elevated sites (gravel terraces) adjacent to the Quillayute physiographic unit. Erosion to the south has resulted in the formation of a steep bluff, and contiguous portions of the Quillayute Prairie support only a fringe of trees; however, to the west and north, where slopes are gentle to moderately steep, forest appears to cover extensive areas formerly occupied by herbaceous vegetation.

Fire was of some recent importance in causing regression of forest at the eastern end of the prairie, but there is no tangible evidence of its influence in the less disturbed western portion. Fire scars are not evident on trees forming the apparent prairie boundary of about a century ago.

At present, the most influential factor in forest encroachment seems to be disturbance of the original prairie vegetation by plowing, burning or grazing. Prior to the advent of agriculture, the forest-prairie boundary, as evidenced by the distinct ecotone observed between climax forest and *Picea* stands in the western section, must have been relatively static. The influence of man, however, has since altered this relationship, and the oldest trees (70-80 yrs in 1953) now on former prairie sites appear to have become established concurrently with the arrival of the first white settlers. Growth rings as wide as 12 mm were observed in *Picea sitchensis* growing along field boundaries, indicating that these recent invaders can make adequate growth on soil of the prairie. One field, not under cultivation since 1925, contained a dense growth of *Picea* to the exclusion of the original herbaceous vegetation, when studied in 1953. Many of these trees were 12-15 m high and 3 dm or more in diameter. Another field, abandoned in 1940, had a scattered stand of *Picea* and *Tsuga* in 1953; all of the trees appeared to be growing vigorously.

A scarcity of seeds does not seem to account for the absence of *Picea* and *Tsuga* seedlings in the western section of the prairie, since there is an ample seed source in the adjacent forest, and

the prevailing wind blows from the forest toward the prairie. Young seedlings might be smothered by the heavy autumn fall of dead *Pteridium* fronds, a situation similar to that described by Schopmeyer and Helmers (1947) for *Thuja* in northern Idaho. In the first report concerning these soils, Whetting (1936) suggested shade and competition as the probable factors preventing growth of tree seedlings. Before white settlers arrived, forest encroachment may have been initiated by the slow, inward invasion and establishment of a few members of certain arborescent species (such as *Picea sitchensis*) along the forest-prairie ecotone, followed by reduced growth and reproduction of prairie species under these trees. This reduction in understory density could facilitate the establishment of increasing numbers of *Picea* and *Tsuga* seedlings, whose subsequent maturity and dense shade production would be inimical to prairie plants. By this slow process of invasion, elimination and establishment, the size of the prairie would gradually be reduced. In recent years, of course, the activities of man have greatly modified this sequence of events.

The abundance of *Picea sitchensis* near the forest-prairie ecotone suggests it as the initial invader, possibly because of a resistance to smothering by *Pteridium*, or because rapid growth reduces the influence of smothering as a factor in its establishment. As *Picea* and other seral species are gradually replaced by the climax conifer *Tsuga heterophylla*, and the forest becomes more open, members of the subordinate climax union (*Polystichum munitum*-*Oxalis oregana*) can invade the habitat successfully.

OTHER SOIL-FORMING FACTORS

Parent Material

The parent material of the Quillayute physiographic unit below about 1 m in depth is light brownish yellow and of silty texture with occasional rounded pebbles about 0.5-2 cm in greatest dimension scattered throughout. At a depth of 3-6 m there is an abrupt transition from this fine-textured material to one of rounded pebbles and gravels. This coarse material is well sorted, rudely stratified and appears to continue downward to the present river level. Evidence such as particle-size analysis and mineralogical suites indicates that the parent material of the entire Quillayute physiographic unit is the same, and that this material is one sedimentary unit.

The parent material for the soils of the Quillayute physiographic unit is derived from the Olympic Mountains. This mountain mass is made up of graywackes, shales and sandstones

that were deposited during the Tertiary period in a marine environment, and later uplifted and metamorphosed to form the land mass from which the mountains were carved. The present landscape is the result of normal erosion and glaciation. Much of the low coastal area consists of glacial drift modified by stream action. Only the higher hills, above about 300 m in elevation, have a residual mantle; lower slopes and intervening valleys contain either glacial drift or alluvium.

The events leading to the formation of the present physiographic unit, which the Quillayute Prairie now largely occupies, may have been as follows:

The deep underlying gravels were deposited by streams during Pleistocene time, when the load-carrying capacity of rivers was greater than at present. The area about the town of Forks is bordered on 3 sides by low hills. These form a depositional basin into which flow 3 rivers: the Bogachiel on the south, the Calawah in the center and the Sol Duc on the north (Fig. 1). These rivers flow from the high country to the east, an area which provided ample material for the streams to transport and deposit in this basin. The high carrying capacity of these streams during late Pleistocene time can be explained on the basis of a steep gradient coupled with large volumes of water provided by melting valley glaciers.

The abrupt separation of rounded gravels from the overlying silty material indicates a sudden change in the depositional environment from a high energy stream to one of low energy. It is postulated that the silty material of the Quillayute physiographic unit was deposited from quiet water in an estuarine environment.

Bretz (1913) and Lupton (1915) cite evidence for shore-line oscillations in the Puget Sound area, with maximum vertical shifts of 90-120 m. A coastal estuary could have formed during one of these subsidences, with the fine sediments then being laid down directly over the coarse gravels. Valley glaciers provided adequate amounts of fine material, and the 3 streams entering the shallow estuary served as transporting agents.

Upon contact with the salt water of the estuary, these fine sediments were flocculated and deposited in the quiet waters. The admixture of small amounts of water-rounded gravel probably resulted from the melting of ice blocks which had gravel adhering to their undersides or distributed within the ice. As the ice melted, the gravel was dropped and mixed with the fine sediment formed by the salting out of the silts and clays. The yellow color of the parent material is caused by

a hydrated iron oxide, probably goethite. Palache *et al.* (1944) state that this oxidized compound may form as a direct inorganic or biogenic precipitate under conditions of temperature and pressure occurring in marine or meteoric waters.

The land was later elevated to its present position, the rivers became erosional rather than depositional agents and nearly all the fine sediments and much of the underlying gravels were removed. Low hills to the north of the Quillayute Prairie prevented destruction of this area by deflecting the course of the Sol Duc River; however, the present land form has been somewhat modified to the north by the Dickey River and Colby Creek.

Climate

The climate of the west coast of the Olympic Peninsula is characterized by cool summers, mild winters, year-long high relative humidity, many rainy days and heavy rainfall with a winter maximum.

At the station nearest the Quillayute Prairie (Forks, about 8 km east), an average yearly precipitation of 116 in. was recorded during the period 1907-1958 (U.S. Dept. Agri. 1941; U.S. Weather Bur. 1939-1958). There was considerable variation during this period, with a minimum of 78 in. and a maximum of 153 in. But even during the driest year, precipitation of less than 3 in. was recorded only for August and September.

Temperatures below 32° F are uncommon and of short duration. Although an extreme of -4° F is on record, minima of 10-25° F are more usual. During the past 20 yrs, the minimum was below 10° F in only two years. Since cold periods rarely extend beyond a week, soils do not freeze to any appreciable depth. Snowfall is generally light; during 8 of the past 20 yrs the seasonal totals have been less than 5 in. However, during the same period, seasonal totals exceeded 20 in. on 6 occasions; there were two record years, each with 48 in. of total snowfall.

Relative humidity is high throughout the year. This humidity results from more than 200 rainy days per year and summer fogs. These coastal fogs, most common during August, are usually dissipated by noon.

Moisture determinations of the surface 15 cm of prairie soil, made during the summer of 1953, indicate that the percentage never went below about 60. However, a high content of organic matter in these same surface horizons also accounts for a high wilting percentage of 33. Precipitation for the area during 1953 was considerably above average; therefore the possibility that

the surface-soil moisture sometimes approaches the wilting point should not be discounted.

Topography

Topography as a soil-forming factor is important chiefly through its control of precipitation runoff. Small to moderate differences in topography have a minor influence on soil formation in humid climates where there is abundant rainfall distributed throughout the year (Thorpe 1942). Only in regions where rainfall becomes a limiting factor for plant growth does topography assume a major role in soil development.

The Quillayute Prairie and adjacent forested area slope very gently to the west. The land surface is gently undulating over the entire study area. Thus it appears that the Quillayute Prairie and associated forest comprise a single physiographic unit. A steep slope occurs near the eastern end of the prairie, but otherwise all slopes on the prairie are less than 10%. Sampling was confined to regions of gentle slope.

Time

The present topography of the Quillayute physiographic unit indicates that erosion has been slight. There are no streams within the prairie and only a few gullies have formed by headward erosion from the margins of the prairie. These gullies are all short (none entirely crosses the prairie) and appear to be stabilized at present; water flows in them only during the wetter months.

The slight degree of erosion of the Quillayute physiographic unit suggests that little material has been removed from the surface since the original deposits were laid down. Soils under the prairie and under the major portion of the surrounding forest vegetation should be in approximate equilibrium with the environment; however, soils in areas of recent forest invasion are currently undergoing more evident transformation.

SOIL PROPERTIES

The entire Quillayute physiographic unit is believed to have supported prairie vegetation early in its development. Nine soil profiles from this physiographic unit were studied in detail (Fig. 2). Of these, two were in the Prairie (sites Q-2 and Q-8), four in the Tsuga forest (sites Q-1, Q-6, Q-9 and Q-10), two in areas recently a part of the Quillayute Prairie but now under Picea forest (sites Q-3 and Q-4), and one in an area believed recently to be under Tsuga forest but now a part of the Quillayute Prairie (site Q-7). Additionally, several transects across

the ecotone were studied. Representative data are presented here. Greater detail for most properties is available (Lotspeich 1956).

Description of the Soil

Only 4 of the 9 profiles studied are described here. Morphological terms are those defined by the Soil Survey Staff (1951). All these soils have a low degree of horizon differentiation below the A_1 , with color as the chief horizon marker. Except in A_1 horizons, structural units are weakly developed. There is no well-defined textural, structural or color B horizon, although under Tsuga a weak structural B_2 was recognized.

Prairie, site Q-2.

- A_{00} , 2.5-0 cm, not sampled: chiefly fronds of *Pteridium*.
 A_{11} , 0-28 cm, sample 7: very dark gray (10 YR 3/2; 2/2, moist) silt loam; crumb structure; roots and rhizomes numerous; earthworms present are of an undescribed species near *Plutellus altmani* Gates, according to D. McKey-Fender, McMinnville, Oregon.
 A_{12} , 28-51 cm, sample 8: dark gray (10 YR 4/1; 2/2, moist) silt loam; subangular blocky structure; roots numerous.
 A_3 , 51-69 cm, sample 9: dark yellowish brown (10 YR 4/4; 3/2, moist) silt; massive breaking into subangular blocks; roots numerous but rhizomes absent.
 AC, 69-84 cm, sample 10: yellowish brown (10 YR 5/8; 4/4, moist) silt; massive breaking into subangular blocks; roots numerous; contact with C is undulating.
 C_1 , 84-109 cm, sample 11: brownish yellow (10 YR 6/8; 5/6, moist) silt; massive breaking into weak subangular blocks; only a few roots present; numerous brown-stained old root channels with vertical orientation.
 C_2 , 109-135 cm, sample 12: yellow (10 YR 7/6; 5/6, moist) silt; massive breaking into weak subangular blocks; few live roots; numerous vertical brown-stained old root channels.

Picea forest, 45-yr-old, site Q-3.

- A_{00} , 2.5-1.3 cm, not sampled: *Picea* needles and moss.
 A_0 , 1.3-0 cm, not sampled: decomposing conifer needles, twigs, and moss.
 A_{11} , 0-18 cm, sample 13: dark reddish brown (5 YR 2/2; 10 YR 2/1, moist) silt loam; crumb structure; zone of maximum root development; many earthworms.
 A_{12} , 18-43 cm, sample 14: very dark grayish brown (10 YR 3/2; 5 YR 2/2, moist) silt; massive breaking into weakly developed subangular blocks; roots present, generally smaller than in A_{11} ; many earthworms.
 A_3 , 43-69 cm, sample 15: dark grayish brown (10 YR 4/4; 3/4, moist) silt; very weakly prismatic; numerous wiry roots (probably *Pteridium*) with vertical orientation.
 AC, 69-99 cm, sample 16: brownish yellow (10 YR 6/6; 5/6, moist) silt; massive breaking into weakly defined subangular blocks; roots numerous; root channels coated with a brown stain; irregular boundary between AC and C horizons.
 C_1 , 99-137 cm, sample 17: yellow (10 YR 7/6; 5/6, moist) silt; massive breaking into weakly defined subangular blocks; brown stained root channels.
 Picea forest, 70-yr-old, site Q-4.
 A_{11} , 0-23 cm, sample 35: dark yellowish brown (10 YR 3/4; 5 YR 2/2, moist) silt loam; crumb structure; zone of maximum root growth.

A_{12} , 23-48 cm, sample 36: dark yellowish brown (10 YR 4/4; 10 YR 3/2, moist) silt; massive breaking into weak subangular blocks; roots present; earthworms numerous in A_1 .

A_3 , 48-71 cm, sample 37: yellowish brown (10 YR 5/4; 10 YR 3/2, moist) silt; very weakly prismatic breaking into subangular blocks; fewer roots but many small root channels.

Climax Tsuga forest, site Q-10.

- A_{00} , 9-4 cm, not sampled: Tsuga needles and cones.
 A_0 , 4-0 cm, not sampled: decomposing needles.
 A_{11} , 0-8 cm, sample 51: dark yellowish brown (10 YR 4/4; 5 YR 3/2, moist) silt loam; granular structure; many roots and earthworms.
 A_{12} , 8-21 cm, sample 52: dark yellowish brown (10 YR 4/4; 7.5 YR 3/2, moist) silt; granular structure; many roots and earthworms.
 AB, 21-38 cm, sample 53: brown (10 YR 5/3; 3/4, moist) silt; weakly developed blocky structure breaking into subangular blocks; many roots; some earthworms.
 B_2 , 38-58 cm, sample 54: brown (10 YR 5/3; 3/4, moist) silt; weakly developed prismatic structure breaking into subangular blocks; inside of aggregates without gray cast; roots numerous; some earthworms.
 B_3 , 58-74 cm, sample 55: pale brown (10 YR 6/3; 3/2, moist) silt; weakly developed blocky structure breaking into subangular blocks; roots infrequent.
 C, 74-104 cm, sample 56: yellow (10 YR 7/6; 5/6, moist) silt; massive breaking into subangular blocks somewhat vesicular; very few roots; numerous small brown stained root channels.

Figure 8 portrays horizons and colors for the 4 profiles described. These 4 plus the other profiles and transects studied, demonstrate that the chief morphological difference between the soils of the prairie and the forest is the color of the A_1 horizons. There tends to be a shift toward more reddish hues under Tsuga. The A_1 horizons tend to become lighter (of higher value) when both dry and moist, and to have a considerably stronger chroma when dry (but not when moist) under Tsuga. Below the A_1 horizons, color contrast decreases with no changes in hue from one site to another.

Horizon thickness and sequence are essentially constant in the prairie, and are not altered by the recent encroachment of *Picea* forest. However, the soil under climax Tsuga forest usually acquires a structural B_2 horizon, and the section over the B_2 was then designated AB rather than A_{12} because of the change in structural type.

In the soil of the prairie most of the *Pteridium* rhizomes are confined to the upper A_1 , but there are many wiry roots throughout the entire A_1 horizon. Under Tsuga, too, the tree roots are concentrated in the A_1 horizon, with only a few in the AB, B_2 , and B_3 horizons. Numerous old root channels, coated with a brown stain, occur throughout the profile under both forest and prairie vegetation.

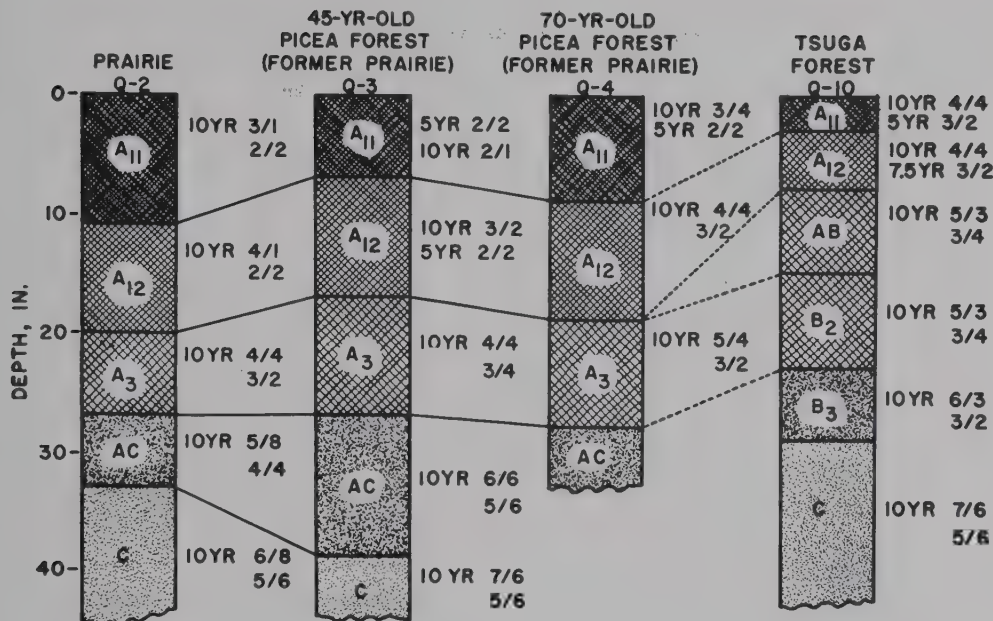


FIG. 8 Diagram of 4 soil profiles showing the close agreement in the thickness of the various horizons of the solums outside the Tsuga forest, but the shift in soil color as the soil of the prairie is invaded by Picea forest. As the latter is replaced by the climax Tsuga forest, the profile develops weak structural characteristics of a B horizon.

The A₁ horizons have a crumb structure under both forest and prairie conditions; however, surface-soil structure shows a weaker development under forest than in the prairie. With increasing depth, the structural units are weak angular or subangular blocks with somewhat better development under the forest. Although the soil-forming material is dominantly massive, there are weak aggregates (subangular blocks) with dimensions of 2-5 mm.

Organic Matter

In each of the profiles from the Quillayute physiographic unit, organic matter decreases rather uniformly with depth until the C horizon is reached. This change is indicated by measures of carbon, nitrogen, and oxidizable material (Table II). Organic matter is still present in significant quantity in the C horizons; the range shown in Table II is from 0.6-1.4% carbon. Additional samples were collected from the soil-forming material by 15-cm increments, until gravel was reached at about 3 m, near each of 3 of the soil profile sites. These were analyzed for oxidizable material. The data, not tabulated, demonstrate reasonable constancy of oxidizable material with depth in the soil-forming material at any one location; among the sites the amount ranged from

near 0.3 to near 1% carbon. Carbon/nitrogen ratios in A₁ horizons are variable but high: 41.3-28.2. These ratios decrease with depth to minimum values of 1.7-3.6 in C horizons.

The only observed correlation between vegetative cover and measured properties of soil organic matter is the higher nitrogen content of A₁₁ horizons under the vegetation of the prairie than under climax Tsuga (sites Q-2 and 8 vs. sites Q-1, 6, 9 and 10). This difference persists in two of the disturbed areas, sites Q-7 and 3. At one site, Q-4, where the vegetation of the prairie was displaced more than 70 yrs ago, the nitrogen content of the A₁₁ horizon is now at the level characteristic of the Tsuga sites.

To check this observed correlation further, 4 soil profiles were examined about 8 km north of the Quillayute Prairie where the soils had developed from residual material under the influence of Tsuga forest with its subordinate *Polystichum* and *Oxalis* vegetation. There is no evidence that this area was ever under prairie vegetation. The carbon content of the surface horizons there was highly variable, with extremes of 6.7 and 14.4% (Table III). This range exceeds that measured for surface samples from sites on the Quillayute Prairie. The nitrogen percentages in surface

TABLE II. Organic matter data for horizon samples of profiles from the Quillayute physiographic unit. These soils are representative of areas of prairie vegetation, former prairie invaded by Picea, climax Tsuga forest, and former Tsuga forest which is now a part of the prairie (area of Gaultheria plus Picea and Tsuga seedlings in Fig. 2)

Sample	Horizon	Depth in cm	Carbon in %	Nitrogen in %	C/N	Oxidizable Material in meq/g	Reactivity in meq/gC
Site Q-2 Prairie							
7	A ₁₁	0-28	12.7	0.73	17.4	37.1	9.5
8	A ₁₂	28-51	9.6	0.47	20.4	26.9	8.6
9	A ₃	51-69	5.5	0.25	22.1	14.0	8.1
10	AC	69-84	2.7	0.15	17.4	6.5	8.0
11	C ₁	84-109	1.4	0.11	12.6	3.5	7.3
12	C ₂	109-135	1.2	0.12	9.6	3.0	6.7
Site Q-8 Prairie							
29	A ₁₁	0-23	14.0	0.74	19.0	36.5	8.8
30	A ₁₂	23-46	11.0	0.52	21.4	29.0	9.2
31	A ₃	46-64	6.1	0.31	20.0	14.9	7.1
32	AC	64-79	3.0	0.18	16.4	7.9	8.5
33	C ₁	79-107	1.0	0.09	11.6	2.7	6.5
34	C ₂	107-132	0.9	0.08	11.0	2.2	6.6
Site Q-3 45-Year-Old Picea							
13	A ₁₁	0-18	15.1	0.78	19.3	41.3	8.1
14	A ₁₂	18-43	8.8	0.38	23.3	24.6	8.3
15	A ₃	43-69	5.1	0.22	23.0	13.2	7.7
16	AC	69-99	1.3	0.09	14.1	3.2	6.9
17	C	99-137	0.9	0.08	10.8	2.3	7.1
Site Q-4 70-Year-Old Picea							
35	A ₁₁	0-23	10.7	0.53	20.0	31.4	10.1
36	A ₁₂	23-48	7.7	0.32	23.7	22.5	9.9
37	A ₃	48-71	5.3	0.24	22.1	14.0	8.6
Site Q-1 Tsuga							
1	A ₁₁	0-8	11.5	0.58	19.9	33.3	12.2
2	A ₁₂	8-23	9.3	0.43	21.7	26.7	11.5
3	AB	23-56	5.8	0.28	21.0	16.2	9.8
4	B ₃	56-69	3.5	0.20	17.4	9.8	8.7
5	C ₁	69-107	1.2	0.08	14.0	2.8	7.8
6	C ₂	107-147	0.9	0.08	11.1	2.2	5.4
Site Q-10 Tsuga							
51	A ₁₁	0-8	12.4	0.59	21.2	33.3	8.3
52	A ₁₂	8-20	9.5	0.50	19.1	26.2	10.5
53	AB	20-38	8.4	0.42	20.1	22.8	10.1
54	B ₃	38-58	6.5	0.31	20.6	17.1	9.4
55	B ₃	58-74	3.5	0.20	16.9	9.0	8.0
56	C	74-104	1.3	0.11	12.0	3.6	8.3
Site Q-9 Tsuga							
44	A ₁₁	0-10	9.3	0.61	15.3	28.2	10.2
45	A ₁₂	10-28	7.9	0.53	14.9	24.2	10.3
46	AB	28-51	6.3	0.38	16.4	18.9	8.8
47	B ₂	51-74	4.7	0.25	18.6	13.2	8.1
48	B ₃	74-97	4.0	0.22	18.3	8.7	6.2
49	C ₁	97-122	1.3	0.11	12.1	3.4	7.2
50	C ₂	122-152	1.1	0.09	11.8	2.8	6.5
Site Q-6 Tsuga							
18	A ₁	0-25	11.3	0.55	20.8	29.2	10.2
19	B ₂	25-48	8.6	0.43	20.0	24.5	7.4
20	B ₃₁	48-69	5.8	0.31	19.1	15.8	9.7
21	B ₃₂	69-99	2.6	0.13	19.3	5.5	6.4
22	C	99-132	0.7	0.06	11.3	1.7	6.3
Site Q-7 Gaultheria, formerly Tsuga							
23	A ₁₁	0-28	10.8	0.61	17.7	28.6	10.1
24	A ₁₂	28-51	7.5	0.36	20.5	19.9	9.1
25	AB	51-66	4.7	0.22	21.1	10.8	6.9
26	B ₃	66-84	3.0	0.16	18.8	6.7	6.8
27	C ₁	84-107	1.0	0.08	13.6	2.5	7.4
28	C ₂	107-127	0.6	0.05	11.7	1.6	7.6

horizons average 0.4, and range from 0.49-0.31. This nitrogen content is lower than that under Tsuga on the Quillayute physiographic unit, but

TABLE III. Organic matter data for samples of profiles under Tsuga about 8 km north of the Quillayute Prairie. Rock underlay deepest sample at each site.

Location	Depth in cm	Carbon in %	Nitrogen in %	C/N	Oxidizable Material in meq/g
D-1	0-15	6.7	0.31	21.7	16.4
	15-31	3.3	0.21	15.9	8.1
	31-61	2.1	0.14	14.6	4.5
	61-71	0.8	0.08	10.4	2.0
D-2	0-15	14.4	0.49	29.4	32.5
	15-31	9.4	0.39	24.0	22.1
	31-46	5.0	0.24	20.8	12.5
	46-61	2.6	0.14	18.5	5.9
D-3	0-15	2.0	0.14	14.1	4.7
	15-31	0.6	0.06	9.2	1.8
	31-46	0.8	0.32	25.1	19.1
	46-56	5.7	0.26	21.8	15.3
D-4	0-15	3.7	0.15	24.9	8.5
	15-31	2.2	0.10	21.5	4.9
	31-46	10.4	0.46	22.7	25.5
	46-61	9.7	0.44	22.0	22.9
	61-71	7.1	0.30	23.6	15.7
		6.0	0.24	25.0	11.2
		3.5	0.18	19.2	7.9

is in line with observed trends of data from prairie to disturbed prairie to Tsuga areas.

To estimate the reactivity of soil organic matter, the hypiodite method, as described by Moodie (1950, 1951), was applied to the soil samples. Hypiodite reacts selectively with certain groups of the organic matter molecule, *i.e.*, phenolic hydroxide and aldehydes. Moodie showed that forest soils are more reactive to hypiodite than are grassland soils. These reactivity indices for the Quillayute soils (Table II) are lower than comparable data reported by Moodie. The data also show that the soils of the prairie and adjacent forest have a similar type of organic matter. Since the high organic matter content of all of these soils indicates a resistant type of organic material, the low reactivity may be the result of limited mineralization of the plant material under the environmental conditions prevailing on the Quillayute Prairie.

Physical and Mineralogical Properties

No important differences in the bulk density of corresponding horizons of soils under forest and prairie vegetation appear in the extensive data collected by Lotspeich (1956). In each profile, bulk density increases gradually from approximately 0.5 g/cc in the A₁₁ to a high of about 1.25 g/cc in the C₂. This latter value is nearly constant among profiles. The low values for the A₁ horizons reflect the influence of the extremely high organic matter content.

Particle-size data were obtained for each of the profiles sampled (Lotspeich 1956); they are

TABLE IV. Mineralogy of the light mineral fraction (sp gr < 2.95) of the very fine sand separate (.1-.05 mm) from horizon samples of profiles under Tsuga and prairie vegetation

Sample	Horizon	Depth in cm	Percentage Distribution of Minerals in Light Fraction of Very Fine Sand						
			Quartz	Orthoclase	Plagioclase	Weathered	Biotite	Chlorite and Muscovite	Pumicite
			Site Q-2		Prairie				
7	A ₁₁	0-28	62	8	23	5	0	1	1
8	A ₁₂	28-51	42	3	38	14	1	1	1
9	A ₃	51-69	26	2	47	24	0	1	0
10	AC	69-84	27	1	40	26	4	2	0
11	C ₁	84-109	29	1	34	30	6	0	0
12	C ₂	109-135	29	1	36	24	7	3	Tr
			Site Q-9		Tsuga				
44	A ₁₁	0-10	56	3	31	8	1	1	0
45	A ₁₂	10-28	53	2	31	13	Tr	1	0
46	AB	28-51	46	5	36	13	0	Tr	1
47	B ₂	51-74	42	4	37	15	1	1	1
48	B ₃	74-96	37	1	39	17	5	1	0
49	C ₁	96-122	32	2	38	19	7	2	0
50	C ₂	122-152	33	4	28	24	9	2	0

not tabulated here. The soils are dominated by the silt separate, which usually ranges from 70-80%, as compared with 85-90% in the soil-forming material. Sand never exceeds 8%, and most of it occurs in the very fine sand separate. Clay content is highest in the A₁₁ (variable but averaging about 20%) and decreases with depth to 6-9% for the deeper horizons. Each profile examined contained small water-rounded pebbles of fine-grained arkose and graywacke scattered throughout the horizons.

Mineralogical studies of the very fine sand separate were made for several profiles. Representative data for light minerals (sp gr < 2.95) show dominance of quartz and plagioclase feldspars in the light mineral suite (Table IV). Quartz/feldspar ratios range from 1-2 in A₁ horizons; they are slightly lower (0.5-1.1) in deeper horizons. Micas constitute only a small portion of the total, with biotite being more important than other micas. The per cent of heavy minerals (sp gr > 2.95) is low in all samples; in no instance is it above 3.7% of the very fine sand separate, with most percentages in the range of 2.1-3.0 (Lotspeich 1956). The heavy minerals are not tabulated; amphiboles are the most important, with epidote next and these two comprise 40-50% of all heavy minerals. Also present, in more than trace quantities, are clinopyroxene, orthopyroxene, clinozoisite, garnet and zircon.

Samples of fine and coarse clay and fine and medium silt from horizon samples of two profiles were analyzed with an X-ray diffractometer. These data (Table V) suggest no significant differences between the two profiles. Minerals with

14Å spacings are present in all fractions of all horizons, and constitute the characteristic clay mineral component of both the fine and coarse clay. Coarse clay fractions of a few samples were examined following potassium saturation, and after heating to 300, 400 and 500° C for 2 hrs. The chlorite-vermiculite designation was chosen since there is some collapse from 14 to 10Å at 300°, but incomplete collapse at 500° C. Since ammonium fixation is negligible (about one meq/100 g) it was concluded that chlorite is dominant over vermiculite.

Since the distribution of total free iron was studied for only two profiles (Table V), the significance of small variations is uncertain. Iron oxide in the soil under prairie vegetation decreases uniformly with depth. For the soil under Tsuga the general pattern is the same, despite small irregularities.

The presence of amphiboles in the silt fractions, and of feldspars in both silt and coarse clay fractions, supports data for mineralogy of the very fine sand in leading to two conclusions. These are (1) the parent material of these soils is a single depositional unit, and (2) mineral weathering has not progressed far, despite strong soil acidity and a favorable climate for alteration.

Chemical Properties

These soils, whether under forest or prairie vegetation, are strongly acid in the A₁ horizons (Table VI); the range in pH, considering all 9 profiles, is 4.6-5.1. The increase in pH with depth is gradual, until values slightly above 5 are reached in upper C horizons. Near 4 sites,

TABLE V. Mineralogy of clay and silt separates and free iron oxide of horizon samples of profiles under Tsuga and prairie vegetation

Sample	Horizon	Depth in cm	MINERALOGY OF PARTICLE SIZES ¹				Free Iron as % of Whole Soil
			Fine Clay < .2μ	Coarse Clay .2-2μ	Fine Silt 2-5μ	Medium Silt 5-20μ	
Site Q-2 Prairie							
7	A ₁₁	0-28	Ch-V	Ch-V, I, Qz, (F)	Ch-V, I, Qz, F	Ch-V, I, Qz, F, A	7.7
8	A ₁₂	28-51	Ch-V	Ch-V, (I), Qz, (F)	Ch-V, I, Qz, F	Ch-V, I, Qz, F, A	7.2
9	A ₃	51-69	Ch-V	Ch-V, —, Qz, (F)	Ch-V, I, Qz, F	Ch-V, I, Qz, F, A	5.3
10	AC	69-84	Ch-V, M	Ch-V, (I), Qz, —	Ch-V, I, Qz, F, (A)	Ch-V, I, Qz, F, A	4.1
11	C ₁	84-109	Ch-V, M	Ch-V, I, Qz, (F)	Ch-V, I, Qz, F	Ch-V, I, Qz, F, A	3.7
12	C ₂	109-135	Ch-V, M	Ch-V, I, Qz, (F)	Ch-V, I, Qz, F	Ch-V, I, Qz, F, A	3.8
Site Q-10 Tsuga							
51	A ₁₁	0-8	Ch-V, (I)	Ch-V, —, Qz, (F)	Ch-V, —, Qz, F, —	Ch-V, I, Qz, F, A	7.7
52	A ₁₂	8-20	Ch-V, —	Ch-V, —, Qz, (F)	Ch-V, I, Qz, F, —	Ch-V, I, Qz, F, A	8.1
53	AB	20-38	Ch-V, —	Ch-V, —, Qz, (F)	Ch-V, I, Qz, F, (A)	Ch-V, I, Qz, F, A	7.8
54	B ₂	38-58	Ch-V, —	Ch-V, —, Qz, (F)	Ch-V, I, Qz, F, (A)	Ch-V, I, Qz, F, (A)	6.9
55	B ₃	58-74	Ch-V, —	Ch-V, (I), Qz, (F)	Ch-V, I, Qz, F, (A)	Ch-V, (I), Qz, F, A	4.6
56	C	74-104	Ch-V, —, M	Ch-V, (I), Qz, —	Ch-V, I, Qz, F, (A)	Ch-V, I, Qz, F, A	3.8

¹ Ch-V=chlorite-vermiculite, M=montmorins, I=illite or mica, Qz=quartz, F=feldspars, and A=amphiboles. Letters in parentheses indicate minerals identified on the basis of a weak peak on the x-ray trace.

samples were collected down to the gravel at about 3 m. The pH of these samples ranged from 5.0-6.1, but at any one site variation did not exceed 0.2 pH unit.

TABLE VI. Reaction, cation exchange capacity and exchangeable cations of horizon samples of profiles under Tsuga and prairie vegetation

Sample	Horizon	Depth in cm	Exchangeable Cations in meq/100g				Cation Exchange Capacity in meq/100g	Base Saturation in %	pH
			Ca	Mg	K	Na			
Site Q-2Prairie									
7	A ₁₁	0-28	0.5	0.3	0.6	0.3	50.3	3.8	4.8
8	A ₁₂	28-51	0.2	0.3	0.1	0.2	41.0	2.0	4.9
9	A ₃	51-69	0.1	0.0	0.0	0.2	28.7	1.0	5.2
10	AC	69-84	0.1	0.0	0.1	0.1	20.1	1.5	5.4
11	C ₁	84-109	0.1	0.0	0.1	0.1	14.9	2.0	5.3
12	C ₂	109-135	0.1	0.0	0.1	0.2	13.6	2.9	5.3
Site Q-1Tsuga									
1	A ₁₁	0-8	0.3	0.4	0.4	0.4	42.6	3.5	4.6
2	A ₁₂	8-23	0.2	0.2	0.2	0.3	35.4	2.5	4.9
3	AB	23-56	0.2	0.0	0.1	0.2	26.4	1.9	5.0
4	B ₃	56-69	0.1	0.1	0.1	0.0	21.6	1.4	5.1
5	C ₁	69-107	0.1	0.1	0.0	0.2	10.4	3.9	5.1
6	C ₂	107-147	0.1	0.0	0.1	0.2	9.3	4.3	5.2

Total cation-exchange capacity of soils both under prairie and Tsuga is high in all horizons having an appreciable content of organic matter (Table VI). The per cent base saturation trends, with maxima in A₁₁ and C₂ horizons, are representative of the more extensive data reported by Lotspeich (1956).

Exchangeable sodium was detected in these soils. Although it never exceeded 0.4 meq/100 g, even this amount is somewhat unusual in a soil

under such a high rainfall. Also, the trend with depth is the reverse of the usual pattern for well-drained soils. Its presence is probably a consequence of the proximity of the Pacific Ocean. The Quillayute physiographic unit is only about 8 km east of the sea, and prevailing winds are from the west. During periods of strong winds salt spray may be carried several kilometers inland, to be deposited on vegetation and soil (Teakle 1937). Sea water contains more magnesium than calcium; this probably explains why several of the soil horizons are higher in exchangeable magnesium than in calcium.

Discussion of Soil Properties

The chief distinguishing characteristics of all of the soils of the Quillayute physiographic unit are the high organic matter content and the lack of horizon differentiation on any basis other than color.

During the examination of the profiles it was noted that many old root channels were present in the C material. Sections of roots collected at depths near 2 m in a recent railroad cut that crosses the prairie were identified as belonging to Pteridium. Since these root channels are also present in the profiles now under forest, this is further evidence for the invasion of the prairie vegetation by trees and not the converse. In no case were live roots noted in the C material of the profiles under forest. The shallow rooting habit of Picea and Tsuga is shown by uprooted trees.

Data from particle-size analyses show that in all the profiles the clay content is highest in the surface horizon, and that there is no horizon of

accumulation below the A. The lack of clay deposition on structural surfaces and pores within the profile is evidence that illuviation has not been significant in these soils. Neither is there apparent any subsurface zone of significant accumulation of oxides.

It is postulated that in the initial phase of soil formation exchangeable bases were probably plentiful, but the cation-exchange capacity was comparatively low owing to the lack of organic matter and the low clay content. In time exchangeable bases were removed by leaching, under the prevailing heavy rainfall, while the exchange capacity was increasing because of the addition of soil organic matter. The high cation-exchange capacity of these soils, as they now exist, is related primarily to the large quantities of organic matter that have accumulated in the soils.

When *Picea* and then *Tsuga* invade the prairie, the soil color changes. Hue remains 10 YR for the surface horizons of the dry soil, but the hue of the wet forest soils is 5 YR. Chroma and value show a more significant change, comparing prairie areas with those under forest. In the dry soil, chroma changes from 3 to 4 in the surface horizon, and value changes from 1 to 4. These are the maximum changes. There are no differences in color of the parent material of the soils under the two vegetative types.

Nitrogen content of the surface-soil horizons in the prairie is higher than that for comparable samples under *Tsuga*. A comparison with samples from a soil developed from residual material north of the Quillayute Prairie confirms the fact that the forest soil characteristic of the region contains less nitrogen than the soil of the prairie.

The crumb structure of the prairie soil is preserved under the forest, but it is less stable than that under the prairie vegetation. Soil acidity does not change appreciably as trees invade the prairie; the range in pH of a forest soil several km to the north of the Quillayute Prairie is similar to that of the prairie and adjoining forest soils.

The soils of the Quillayute Prairie and adjoining forest do not have a place in the present soil classification system of the United States Department of Agriculture. A podzolic soil forms under *Tsuga heterophylla* in northern Idaho and northeastern Washington. Podzolic soils also occur in western Clallam County, but only at higher elevations. Although in a more northerly latitude than some podzolic soils in eastern United States, the soils of the Quillayute physiographic unit have formed in a humid, temperate climate where a prolonged snow cover seldom exists.

SUMMARY

Vegetation as a soil-forming factor was studied under forest and prairie conditions on the Quillayute physiographic unit in the western part of the Olympic Peninsula, Clallam County, Washington. This physiographic unit consists chiefly of the Quillayute Prairie, with an adjacent narrow forested strip to the north, east and west. Beyond the boundaries of the physiographic unit the landscape is also forested.

The soils and vegetation of this physiographic unit are developing under a temperate humid climate on a silty sediment deposited in a postulated estuarine environment. This material is glacial flour from the valley glaciers that were present in the western Olympics during late Pleistocene time. The source rocks are of Tertiary age and are composed chiefly of shales, graywackes and arkoses.

The vegetation of the prairie is chiefly herbaceous and is dominated by *Pteridium aquilinum* var. *pubescens*. In the adjacent climax forest *Tsuga heterophylla* is the dominant arborescent species. It is believed that the prairie vegetation once covered the entire physiographic unit, and that plants of the climax forest were encroaching only with extreme slowness prior to disturbances introduced with agriculture. Evidence is presented for expansion of the prairie vegetation as a result of clearing and burning of the forest, and for expansion of the forest vegetation as a result of abandonment of plowed portions of the prairie. *Picea sitchensis* is shown to be a one-generation seral species in these latter areas.

In the Quillayute physiographic unit soils are characterized by a high organic matter content in the surface horizon, and consequently by a high cation-exchange capacity. The entire profile is strongly acid, with a low degree of base saturation. Weathering of soil minerals in place does not appear to have taken place to any appreciable extent. There is no subsurface horizon of accumulation of silicate clays or of oxides. Horizon differentiation is based almost solely on color differences related to soil organic matter.

The chief differences between the soils of the prairie and adjacent forest are color and composition of the organic matter. Color changes from the very dark gray of the prairie to dark reddish brown after trees invade the prairie. Organic matter content is little different under the contrasting plant communities but the soil of the prairie does have higher nitrogen percentages than those found in comparable near-surface horizons under forest.

The soils of the Quillayute physiographic unit do not possess features of a podzolic soil other than an acid reaction, although they do occur in a latitude and under a forest vegetation where podzolic soils are commonly formed.

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GEOGRAPHIC VARIATION IN REPRODUCTION, SIZE, SEX RATIO AND MATURITY OF *STERNOTHAERUS ODORATUS* (TESTUDINATA: CHELYDRIDAE)

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INTRODUCTION

Little information is available on variation in clutch size, in body size and in age or size at attainment of maturity in North American reptiles. The literature contains scattered notes on the

number of eggs found in turtle nests or within females in various parts of the country, but seldom have large numbers been examined, and the published data often are not comparable.

The data presented here were obtained during

a study of geographic variation in shell morphology of the common musk turtle (*Sternotherus odoratus*) based primarily upon museum collections. I am indebted to the Texas Technological College Office of Research for supporting some phases of the study and to the following institutions and individuals for the loan of material: Charles M. Bogert, American Museum of Natural History; Fred R. Cagle, Tulane University; William Riemer, University of Florida; W. Frank Blair, University of Texas; Hobart M. Smith, University of Illinois; Neil Richmond, Carnegie Museum; John Legler, University of Kansas; Norman Hartweg, University of Michigan. For field assistance I am particularly grateful to Robert Webb, University of Kansas and Whitfield Gibbons, Tuscaloosa, Alabama.

PROCEDURE

The states from which material was examined were combined somewhat arbitrarily into southern and northern groups for the purposes of comparing northern with southern populations. Reproductive data were obtained from 200 of the 838 turtles examined in this study. These turtles were from the following states: *Northern*—Connecticut, 1; Illinois, 9; Indiana, 2; Kansas, 10; Maryland, 1; Michigan, 19; New Jersey, 6; New York, 1; Pennsylvania, 25; *Southern*—Alabama, 12; Arkansas, 8; Florida, 45; Georgia, 18; Louisiana, 17; Tennessee, 2; and Texas, 24.

Turtles were opened by sawing through the plastral bridges and partially removing the plastron. The condition and size of the testes and vasa deferentia were noted, and the ovarian follicles greater than 5 millimeters were counted and, in many cases, measured. The oviducal eggs and corpora lutea were counted and the condition of the oviducts and their size were noted. Measurements of reproductive structures were made to the nearest millimeter with dividers; measurements of portions of the turtle shell were made with vernier calipers to the nearest millimeter.

RESULTS

Geographic variation in clutch size

In determining clutch size it was assumed that all eggs present in the oviduct of a turtle represented a single clutch, but whether this is or is not true is of little consequence. Thirty southern and 15 northern turtles contained eggs in the oviducts; the average number of eggs in southern turtles was 2.2 (1-4), in northern turtles, 4.6 (2-7).

The clutch size of birds and the litter size of mammals average higher in cooler climates and

more northerly latitudes (Lack 1954). The same is true in *Sternotherus odoratus* and it is tempting to speculate that this larger clutch size of northern turtles has arisen because of higher mortality that may occur in the north, particularly during extended hibernation. However, as Lack has pointed out "if one type of individual lays more eggs than another type and the difference is hereditary, then the more fecund type must come to predominate over the other (even if there is overpopulation)—unless for some reason the individuals laying more eggs leave fewer, not more, eventual descendants." Thus, it can be claimed that if mortality is greater in the north, a turtle coming from a large clutch has survival value over those in a smaller clutch, and consequently turtles laying large clutches may come to predominate in the population. However, this does not explain the small clutch size of southern turtles because natural selection cannot favor a small clutch size except for reasons noted above. The turtles from large clutches in the south should have at least equal survival value with those from small clutches, other factors being equal.

Without attempting an explanation, there are factors that may be related to small clutch size in southern populations. The southern female turtles reach sexual maturity earlier and may have a longer reproductive life, and the southern turtles are smaller. These 2 factors will be discussed in detail. Other factors that may be operating on clutch size in southern populations are continual overpopulation which would favor smaller clutches, greater survival of turtles from small clutches than from large ones, and larger eggs with greater yolk than in the north which would give the southern young survival value over those from larger clutches and smaller eggs. No data are available on any of the last 3 possibilities, except a note by Risley (1933) recording the fact that 9 eggs taken from a female *Sternotherus odoratus* were of minimum size compared to 3 large eggs taken from a much smaller female.

Some information is available in the literature on clutch size in *Sternotherus* and other turtles. Risley (1933) reported that the clutch size in Michigan varied from 2 to 7, but was usually 3 to 5. Newman (1906) mentioned that no female opened by him in northern Indiana contained more than 3 oviducal eggs. Cahn (1937) reported that the normal egg complement in Illinois was 3, but that occasionally 4 or 5 are encountered. Babcock reported that clutches in New England contained 3, 5 or sometimes 7 eggs. Cagle (1937) noted an average of 2.3 eggs in 4

nests of this species at Reelfoot Lake, Tennessee. Cagle (1954) observed that the average clutch size in 48 specimens of *Chrysemys picta* was 6.3 (3-8) in Illinois and 4.3 (3-6) in 13 Tennessee specimens. Cagle (1950) found that the average number of eggs in the nests of *Pseudemys scripta* was lowest in Louisiana (7.0) and higher in Illinois (9.3) and Tennessee (10.5). Most of these data indicate a generally higher average clutch size in northern than southern turtles.

The data of Fitch (1958) on clutch size in the lizard *Cnemidophorus sexlineatus* indicate that females in northern populations lay larger clutches than those in more southerly areas. However, Fitch pointed out that differences in age composition of females in these populations may be more important than latitude. The same author (Fitch 1954) presents data that indicate greater clutch size in northern than southern populations of the lizard *Eumeces fasciatus*.

Correlation of clutch size and body size

In many species of reptiles, larger females on the average produce larger clutches; this has been reported in the turtle *Pseudemys s. elegans* by Cagle (1944, 1950) in Illinois, Tennessee and Indiana, but the same author (1954) found no such correlation in painted turtles (*Chrysemys picta*). Einem (1956) reported larger numbers of oviducal eggs in larger female *Kinosternon bauri bauri* than in smaller ones.

The *Sternotherus odoratus* were divided into 2 arbitrary size groups of 61-90 mm and 91-120 mm. The average clutch size in the first group was 2.0 in southern turtles, 3.5 in northern turtles. Therefore, in this size range the clutch size in northern turtles exceeds that in southern ones by 75%. Females in the size group of 91-120 mm lay an average of 3.2 eggs per clutch in the south, 5.5 in the north; clutch size in this size range is 72% greater in northern than in southern turtles. In southern turtles, individuals in the larger size group average 60% larger clutches than southern turtles in the smaller size group; in northern turtles this figure is 57%.

It is obvious from the above that northern turtles are more productive even when similar size groups of northern and southern turtles are compared. If selection for larger sized individuals in northern turtles is coupled with selection for individuals with a higher reproductive potential, the net gain in clutch size would be greater. There are indications that such a coupled selection does occur.

Twenty-eight southern males were examined for signs of maturity. The criteria of maturity were testes enlarged to a certain size, an enlarged

and convoluted vas deferens or the presence of tailed spermatozoa in the testes or in the vasa deferentia. The smallest mature southern male was 54 mm in carapace length (straight-line measurement); the largest immature male was 59 mm. The average size of mature males was 65 mm. Of 11 northern males examined, the smallest sexually mature individual was 63 mm, the largest immature turtle was 66 mm, and the average size of mature males was 73 mm.

Eighty-six southern females were examined for signs of sexual maturity such as yolk-filled ovarian follicles of a certain size, ovulation scars in the ovary or eggs in the oviduct. The smallest mature female was 61 mm in carapace length, the largest immature turtle was 78 mm and the average size of adult females was 82 mm. The smallest mature female of 64 northern specimens examined was 80 mm, the largest immature was 88 mm and the average size of adults was 96 mm. Risley (1933) did not discuss the size at sexual maturity in *Sternotherus odoratus* in Michigan, but from his comments concerning age at maturity and from his growth figures for age classes one can extrapolate the information that males reach maturity at a size near 60 mm while females reach maturity at a carapace length near 80 mm; these data are reasonably close to those derived from this study. Cagle (1942) recorded 81 mm for the youngest female *S. odoratus* found to contain eggs in southern Illinois.

Northern turtles as adults thus average larger than southern ones and must reach, generally, a greater carapace length before attaining maturity. Cagle (1950) found no such difference in size required for maturity in *Pseudemys scripta* in Illinois, Tennessee and Louisiana populations, but the same author (1954) has shown that the size at maturity in Louisiana populations of the painted turtle (*Chrysemys picta*) is considerably less (5.5 cm) than in Illinois (7 cm) and Michigan (9 cm) populations.

A few records are available on size maxima of *S. odoratus* in several areas. The largest recorded by Conant (1938) in Ohio was 127 mm in carapace length; by McCauley (1945) in Maryland, 103 mm; by Evermann and Clark (1916) in Indiana, approximately 136 mm; and by Risley (1933) in Michigan, 122 mm.

The minimum size at maturity in any male *S. odoratus* was 54 mm, in any female, 61. Therefore, I compared the northern and southern males greater than 50 mm in carapace length and all females above 60. (Figures 1 and 2.)

If the selection for larger sized females in the north is related to their ability to lay larger

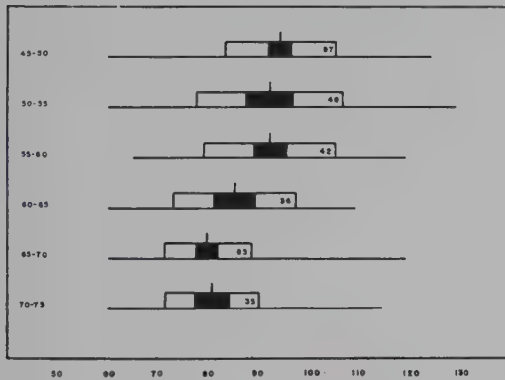


FIG. 1. Comparison of the carapace length in millimeters of female *Sternotherus odoratus* (abscissa) from six isotherm zones. Each bar diagram shows the range, mean, 1 standard deviation, 2 standard errors, and the number of specimens.

clutches of eggs necessitated by higher mortality in the northern populations, then graphing size increase in turtles by isotherm zones may indicate how size is related to increasingly harsher environmental conditions where mortality is likely to be higher. The isotherms are taken from the maps presented in the Yearbook of Agriculture (1941). Female turtles between isotherms 65 and 75 are significantly different in mean size from all those above isotherm line 55. Females between isotherms 60 and 65 are intermediate in size between the two groups. The most significant increase in mean clutch size occurs above isotherm 60. In males there is a steady cline in body size from south to north except for a reversal above isotherm 50 in mean carapace length. However,

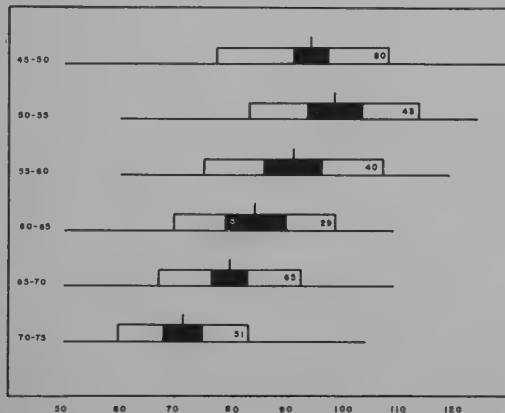


FIG. 2. Comparison of the carapace length in millimeters of male *Sternotherus odoratus* (abscissa) from six isotherm zones. Each bar diagram shows the range, mean, 1 standard deviation, 2 standard errors, and the number of specimens.

this discrepancy is statistically insignificant ($t = 1.6$). The mean size of males between isotherms 70 and 75 is significantly different from those of all other isotherm groups. The mean size of males between isotherms 65 and 70 is significantly different from all other groups except those between isotherms 60 and 65. The means of males from the more northerly populations between isotherms 45 and 60 are not significantly different from one another, but in these groups there is a trend toward greater carapace length, reversed only above isotherm 50. Figures 1 and 2 verify the conclusion that southern turtles are, as a group, somewhat smaller than those in northern populations.

Sexual dimorphism in body size

In many species of turtles, particularly of the genus *Graptemys* the females attain a much larger size than the males. Figures 1 and 2 show that there is little or no difference in the mean sizes of males and females except in the most southerly populations. The range in size and maximum size attained are similar. Risley (1930) reported no significant differences in size of the 2 sexes examined in his study of Michigan *Sternotherus odoratus*.

Correlation of clutch size and isotherm zones

Although few turtles were available for dissection from some of the isotherm zones, the data show a remarkable correlation of increasing average clutch size with more northerly isotherms (Table I).

TABLE I. The mean clutch size of turtles from several isotherm zones

Isotherm Zone	Mean Clutch Size	No. of Specimens
70-75	1.8	8
65-70	2.3	22
60-65	2.8	4
55-60	3.0	2
50-55	3.5	2
45-50	5.5	10

It is fortunate that the most reliable data are available from the most northerly and most southerly isotherm zones for these data show clearly that the average clutch size is tripled from 1.8 between zone 70 and 75 to 5.5 between zones 45 and 50. These data are strengthened by the fact that reproductive potential, for which there are more data, shows exactly the same trend.

Reproductive potential

The term reproductive potential as used in this paper refers to the partial potential reproductive

capacity of Allee *et al.* (1949). This maximum potential can be determined by counting the number of large yolk-filled follicles that could be ovulated during one season and by adding to this the number of eggs already in the oviduct and/or the number of ovulation scars in the ovaries. In this study it was found with few exceptions, that only corpora lutea representing recent ovulations were macroscopically visible. The corpus luteum in a turtle probably has little or no endocrine function and it degenerated rapidly after ovulation. No microscopic examinations of ovarian sections were made to determine whether old scars could be found in this manner.

In females collected during the early part of a year, reproductive potential must be calculated solely by counting the total number of enlarged, potentially ovulatory follicles. During the season of ovulation and oviposition the number of oviducal eggs or corpora lutea was added to the number of remaining large follicles to estimate potential. In a female taken just after the reproductive season, few enlarged follicles will be present whereas most of the complement of enlarged follicles will be present in a winter female indicating that considerable follicular enlargement takes place during the fall and early winter. A postreproductive female is therefore not a reliable source of information on potential because the corpora lutea that might indicate the number of eggs ovulated have disappeared and the follicles to represent the next years complement have not yet enlarged.

Altland (1951) reported from a study of the reproductive tracts of the box turtle that the growth of oogonia begins in July and August and soon results in follicles of various sizes, but some of the potentially ovulatory follicles for the succeeding year were formed as late as September or October. This author also points out that follicular atresia would not nearly account for the loss of all follicles that fail to mature and be ovulated; on this basis he suggests that some of the enlarged follicles formed during one reproductive season may be held over to the next. Cagle (1944) showed that enlarged follicles were present throughout the year in adult slider turtles (*Pseudemys scripta elegans*) with the only change in gross appearance of the ovary being a gradual increase in follicle size which "advances one set to ovulatory stage each season." Einem (1956) reported enlarged follicles in *Kinosternon b. bauri* in postreproductive females.

In view of these reports supported by similar observations in the present study it would seem that there is no means by which the reproductive

potential can be exactly calculated, particularly since some turtles are known to produce more than one clutch per year. However, counts of follicles, lutea and eggs will give an estimate of the maximum egg production and these maxima can then be compared, but the actual production may be much lower.

For comparison, the turtles were first divided into groups representing the same north and south divisions discussed in relation to clutch size. The average potential in prereproductive and postreproductive females was calculated and the percent realization of potential determined (Table II).

TABLE II. Reproductive potential, clutch size and percentage realization of potential in northern and southern *Sternotherus odoratus*

Geog. Area	Avg. Prerep. Potential	Avg. Clutch Size	% Realization	Avg. Postrep. Potential	% reduction from prerep. potent.
North....	10.8	4.3	39.8	9.1	15.7
South....	4.2	2.5	59.5	3.2	23.8

No specimens of southern turtles were available with enlarged follicles from early enough in the year to calculate prereproductive potential, so data from turtles collected during March and April were utilized because most southern turtles have not begun ovulation during these months. It is evident that the reproductive potential, like clutch size, is considerable greater in northern than in southern turtles, but the percentage realization of potential is higher in southern populations, assuming that these figures are reliable.

If no new enlarged follicles were added to the ovary during a single season, the mean number of enlarged follicles in the postreproductive ovaries should be nearly equal to the mean number in the prereproductive ovary minus the mean number of eggs or lutea. Because this is not the case, it follows that new follicles are enlarged during the summer and may be held over for ovulation the next year as suggested by Altland (*op. cit.*).

A few turtles (Hildebrand 1929) are known to lay more than one clutch of eggs in a single season and other species are suspected of laying multiple clutches (Cagle 1950, 1954; Einem 1956). If this were also true of *Sternotherus odoratus* it would apply almost necessarily to southern populations because of the short reproductive season in the north (see section on egg laying season) and it would compensate for the low clutch size of southern turtles. However, I have no evidence that *S. odoratus* produces more than a single

clutch in any part of its range; the only slight indication of this might be the fact that the number of enlarged follicles in postreproductive southern females is 66% greater than in northern ones. This indicates the potentiality for laying 2nd, and slightly smaller, clutches, but no such conclusion can be drawn from other observations. Risley (1933) comments that he has never found any evidence of the 2nd ovulation or oviposition within a single year in Michigan *S. odoratus*.

If *Sternotherus odoratus* lays but one clutch per year, the average reproductive potential for all southern turtles examined was 4.9 with a 51% realization of potential and 9.5 for northern individuals with 45% realization.

The reproductive potential, like clutch size, increases as one samples turtles from farther north. This trend is shown clearly in Table III in which reproductive potential is shown for each isotherm zone.

TABLE III. Reproductive potential in *Sternotherus odoratus* and the percentage realization of potential in six isotherm zones

Zone	Mean Reproductive Potential	No. of specimens	% Realization
70-75.....	3.2	6	56%
65-70.....	4.7	26	49%
60-65.....	5.9	9	47%
55-60.....	8.2	13	37%
50-55.....	9.7	7	36%
45-50.....	10.8	20	51%

The average reproductive potential for isotherm zones 45-50 is 10.8, more than 3 times that of the most southerly zones. This is almost exactly the same average percentage increase as shown for clutch size. The realization of potential shows a steady decline as one proceeds north, but this trend is reversed above isotherm 50 where the realization is about the same as that of turtles from the most southerly isotherm zone.

There is a direct correlation between reproductive potential and increased carapace length (Figure 3). It can be seen by examination of this figure that an increase in carapace length by northern turtles is associated with a much more rapid increase in reproductive potential than is true of southern turtles. The lines drawn through the dots in the figures represent rough regression lines placed by the thread method of Klauber (1943).

Egg laying season

The egg laying season can be delimited by opening turtles from all months of the year and determining those in which eggs are present in the

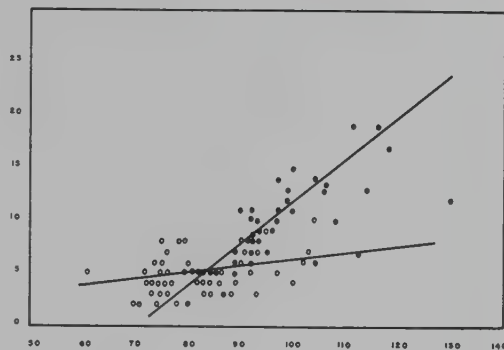


FIG. 3. Correlation of carapace length in millimeters (abscissa) with the reproductive potential (ordinate). Open circles are southern turtles, solid circles are northern.

oviducts or when fresh luteal scars are present in the absence of recently deposited eggs. These results are shown in Table IV.

TABLE IV. Numbers of adult specimens with and without eggs taken during the spring and summer from northern and southern populations

Month		Southern	Northern
March.....	No.	1	1
	With eggs	1	0
April.....	No.	4	4
	With eggs	4	0
May.....	No.	4	17
	With eggs	2	8
June.....	No.	29	7
	With eggs	21	5
July.....	No.	8	2
	With eggs	5	0
August.....	No.	223	2
	With eggs	0	0

The egg laying season in the south begins earlier and lasts longer (March-July) than in the north (May-June). The long southern season might make it possible for a southern turtle to ovulate twice during a single season, but not the short northern season. As noted earlier, however, there is little evidence of multiple ovulations in southern females. No information is available in the literature on the egg-laying season of southern *S. odoratus*, but published information from northern states indicates a short period. Smith (1950) recorded this period as early to middle summer in Kansas and Risley (1933) stated that the egg-laying season extends from the last 20 days of June through the first 5 days of July in Michigan with ovulation first occurring near mid-May. Newmann (1906) reported that nesting in Indiana begins in early June "and lasts nearly the entire month." Babcock (1919) says

that laying in New England occurs in June as does Cahn (1937) in Illinois.

Sex Ratios

The ratio of males to females in turtles may have considerable bearing on reproductive success. Hildebrand (1929), in extensive experiments with the artificial propagation of diamond-back terrapins (*Malaclemmys*), has shown that egg fertility in females is higher when there is a high proportional number of males to females in experimental populations.

Risley (1933) has reported a widely disparate sex ratio in 255 specimens of Michigan *Sternotherus odoratus* of 1.0 male per 2.3 females. If his figures are broken down by season, it is shown that females always outnumber males in the samples. In 226 specimens of this species examined by Cagle (1942) in southern Illinois, the females outnumbered the males, but much less significantly, as the males comprised 41% of the samples. The sex ratio of *Malaclemmys* reported by Hildebrand (1929) show an even greater deviation in favor of females, the ratio in 1300 specimens being 1 male to 4.4 females. Almost all reports of sex ratio in turtles suggest that the females outnumber the males. This was not the case however in 2 of 5 species studied by Cagle (1942), but the samples of these 2 were rather small for definitive knowledge of the sex ratio. The same author (Cagle 1950) reported an approximate 1:1 ratio of the sexes in *Pseudemys scripta* adults, but a ratio of almost 2:1 in favor of females if all turtles in which sex could be determined were included. In a study of 3 other species of the genus *Sternotherus*, Tinkle (1958) showed that the sex ratio was approximately equal in 2 species, except for favoring females in the larger size groups, but that the ratio in the 3rd species (*S. depressus*) was 24% males and 76% females with females predominating in all samples collected.

The determination of sex in very small specimens of *S. odoratus* is difficult. In one large series of 51 specimens from a single locality in Alexander Co., Illinois there were 36 females and 15 males, a ratio of greater than 2:1 in favor of females and very near that reported for this species by Risley (*op cit.*). However, as sex was difficult to determine accurately in these small turtles which were for the most part less than 25 mm in carapace length, no significance is attached to these figures. Of 647 turtles over 50 mm in carapace length in which sex could be determined with certainty, 339 (52%) were females and 308 (48%) were males, which is not significant ($\chi^2 =$

0.16). Table V shows the sex ratio of turtles in different isotherm zones. Females tend to show a slight predominance, but not a significant one. No geographic trends in sex ratio are evident.

TABLE V. Percentage of each sex in large numbers of *Sternotherus odoratus* from six isotherm zones

Zone	No. Males	% ♂♂	No. Females	% ♀♀	Total
70-75.....	51	59%	35	41%	86
65-70.....	65	44%	83	56%	148
60-65.....	29	45%	36	55%	65
55-60.....	40	49%	42	51%	82
50-55.....	43	48%	46	52%	89
45-50.....	80	45%	97	55%	177

These ratios are based upon pooled samples from widely scattered populations and may not reflect differences in sex ratios that may exist in some populations or some areas. However, with the material at hand no clearer picture of sex ratios is likely to be obtained by considering only large series from single localities or from a single season, for sex ratios in musk turtles may be different from one season to another, perhaps reflecting in part seasonal activities of the turtles (Tinkle 1958).

Size and age at sexual maturity

The minimum size at maturity of southern male *S. odoratus* was 54 mm (mean = 65 mm) while that of southern females was 61 mm ($M = 82$ mm). Comparable figures for northern males and females are 63 mm ($M = 73$ mm) and 80 mm ($M = 96$ mm), respectively.

The age at which maturity is reached is more difficult to determine. It has not been established that the rings in the carapacial shields and plastral scutes of sternotherine turtles are actually laid down annually; these rings are reliable age indicators in some turtles (Cagle 1946). Counts of these rings, actually irregular concentric ridges, are difficult to make in musk turtles because they are rapidly worn off by bottom-crawling activities so that, the larger the turtle, the less accurate counts of these ridges will be. Accurate counts could be made in only 46 turtles. Assuming that these are reliable indicators of age, certain conclusions can be drawn concerning age at maturity.

No mature northern female had less than 3 annuli and most had 4 or more. The oldest immature female examined had 7. The youngest mature northern male had 3 annuli, but several with this number were immature. The oldest immature male also had 3 annuli, so the age at sexual maturity for northern males can be set

more certainly at 3 years. The youngest mature female in the south had 2 annuli. No specimens were available with more than 3 annuli, but all those with 3 were adults. Several with one or 2 annuli were immature, so the age at maturity is approximately 3 years. The youngest mature southern male had 3 annuli and none with more than 3 was immature. One with a single annulus was mature, but all others with one or 2 were immature. Therefore, the average age at sexual maturity in southern males is 3 years, as in the north.

The data with regard to age at maturity in northern male *S. odoratus* agree with those of Risley (1933) who found that most of those in Michigan reached maturity at an age of 3 to 4 years. However, Risley concluded that northern females did not reach maturity until their 9 to 11 years. I feel that this figure is too high and probably results from counting pseudo annuli resulting from seasonal growth stoppages in some turtles. The sizes and ages at maturity of all the species and races in the genus *Sternotherus* have now been estimated and are summarized in Table VI; the data on other species are from Tinkle (1958).

TABLE VI. A summary of the ages and sizes at maturity of sternotherine turtles

Species	SIZE		AGE	
	Females	Males	Females	Males
<i>carinatus</i>	100	100-120	4-5	5-6
<i>depressus</i>	90-100	75	over 4	4
<i>m. minor</i>	80	80	5-5	4-7
<i>m. peltifer</i>	90-100	60-70	6-8	3-4
<i>odoratus</i>	80-95	60-70	2-7	3

As with most turtles in which age at maturity has been determined, the females usually require longer to reach maturity.

There are not sufficient data available to evaluate how age composition of musk turtles in northern and southern populations is related to reproductive potential or clutch size.

SUMMARY AND CONCLUSIONS

1. The average clutch size of northern *Sternotherus odoratus* (4.6) is greater than that of southern turtles (2.2). Explanations for this difference may lie in higher mortality in the north, but this does not explain the small clutch size in southern turtles.
2. There is a significantly higher clutch size in large than in small turtles in both northern and

southern populations. Available literature indicates that this is true of most turtles.

3. Northern turtles usually average larger than southern ones, but not enough to explain their larger clutch size. This general increase in size may be seen when turtles are plotted by isotherm zones.
4. Both southern males and females reach sexual maturity at a smaller size (carapace length) than do the northern sexes. The age at maturity is about the same for northern and southern males, but southern females mature earlier than northern ones. Other data on other species of *Sternotherus* show that males usually mature earlier than females.
5. There is little sexual dimorphism in body size in *S. odoratus*, but what little does exist is more strongly indicated in extreme southern populations.
6. Reproductive potential is difficult to estimate, but comparable figures for maximum potential can be obtained. Reproductive potential is directly proportional to increasing carapace length and, like clutch size, is higher (as much as 3 times) in northern than southern populations and shows a steady increase proceeding northward in each isotherm zone. The average for northern turtles is 9.5 and for southern, 4.9.
7. There is no evidence of either northern or southern turtles laying more than one clutch per year, but if it does occur it would be restricted to southern populations because of the short northern egg-laying season.
8. The egg laying season extends from March through July in the south and from May through June in the north.
9. The sex ratios of all turtles examined in which sex could be determined was skewed in favor of females, but not significantly. Most reports on turtle sex ratios that are based on large numbers indicate a predominance of females, sometimes as high as 4:1. One large sample of young *S. odoratus* hatchlings showed slightly more than a 2:1 ratio in favor of females.

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STUDIES ON THE MIGRATION OF THE MONARCH BUTTERFLY I. BREEDING POPULATIONS OF *DANAUS PLEXIPPUS* AND *D. GILIPPUS BERENICE* IN SOUTH CENTRAL FLORIDA

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INTRODUCTION

The phenomenon of migration in animals includes at least 3 distinct types of movements of individuals from one place of residence to another, as pointed out by Allee *et al.* (1949). True migration is a periodic journey of the same individuals back and forth between 2 areas. In some animals such as many birds and several mammals this involves the movement of a population to an area where the food supply is seasonally abundant and where the young are produced and reared, followed by a return of the parents and their offspring to a climatically more equitable locality in which they overwinter without reproducing. In other animals, including several fish, the young are born in one area, travel to another, and then

return to their birth places to produce the next generation. Contrasting with true migration is remigration in which none of the individuals comes back to the original area, the return movements instead being made by individuals produced in later generations. The distinction between these 2 types is important, since in the first the possibility exists that the movement in at least one direction involves learning whereas, in remigration, movement in both directions has to be based completely on genetic inheritance. The 3rd type of animal movement is called emigration and its converse, immigration. In this, the animals move in a one-way direction, from one place to another, there being no return either of the same individuals or of those produced in later generations.

The studies of Williams and his co-workers, reviewed in his new book (1958), have led to the general acceptance that the periodic movements of the Monarch butterfly, *Danaus plexippus* (Linné), represent true migration similar to that found in fish as mentioned above. Accordingly, it is thought that the adult butterflies travel southward in the fall, overwinter without breeding, fly northward in the spring, laying eggs as they proceed, and finally die (cf. Beall 1941). As such, the fall journey is composed of individuals which are one or more generations removed from their northward-bound forebearers, the precise number being unknown, although most certainly varying at different latitudes.

The purpose of the present paper is twofold: first, to reconsider the migration of *Danaus plexippus* in the light of our discovery of breeding populations in its southeastern overwintering range in North America; and second, to relate the Monarch's winter populations with those of an ecologically similar species, *Danaus gilippus berenice* (Cramer), the Queen, with which it is sympatric during the overwintering portion of its annual migration cycle.

AREAS AND TIMES OF STUDY

Breeding populations of the Monarch and Queen were discovered in south central Florida during the spring of 1956 while we were engaged in research at the Archbold Biological Station. In 1959, we returned to this region to follow up the earlier findings and discovered several additional breeding populations. The locations of the 4 places discussed below are indicated in Figure 1.

The area most intensively investigated is located in Highlands County, Florida about 4 miles

south of Highlands Hammock State Park (Area No. 1, Lat. 27° 25' 0" N; Long. 81° 30' 55" E.). Here in the midst of a once-lumbered pine and scrub association, about 7 miles west of the sand ridge that runs north and south through central Florida, there is a concentration of the milkweed, *Asclepias humistrata* Walt. This plant is one of several *Asclepias* species which is suitable as larval food for both the Monarch and Queen and we found it particularly abundant in an area of about 10 acres. Approximately one-fourth of this consists of land on which an early 20th century lumber camp existed. This area and the bordering scrub woods were cleared and harrowed shortly after the spring data were collected in 1959. By June the milkweeds had recovered. Another fourth is a poorly cultivated orange grove, while the remaining half is a pasture meadow, which was cleared, harrowed and planted in the early 1950's with a species of range grass, as yet undetermined. Three other species of milkweed also occur here, although less abundantly than *A. humistrata*. The most common of these is *A. tuberosa rolfsii* (Britton) Woodson, a medium-sized plant with a few erect stems. It prefers slightly less open situations than *A. humistrata*, a large and many-stemmed sprawling plant which grows in bare sand patches among the grass. The remaining 2 species, *A. tomentosa* Ell. and *A. curtissii* A. Gray, are like *A. rolfsii* in size, erectness, and habitat but both were so uncommon that their role as food for the butterflies was far less important. The frequencies of the four plant species in July 1959 were very roughly 100: 25: 4: 1, in the order mentioned above. It might be added that because of its size, one *A. humistrata* plant can provide far more larval food than one of the other plants. The quantitative relationships of these plants as food will be considered in a later paper.

In addition to obtaining data here in the spring of 1956, collections were made in 1959 between March 25th and 31st, and then at weekly intervals from the 15th of June through August 4th.

During the spring and summer of 1959, collections were made in a 2nd area about 15 miles southeast of Area 1 on the western edge of the sand ridge mentioned above (Area No. 2, Lat. 27° 13' 15" N; Long. 81° 20' 36" E.). Here on the eastern side of Lake Childs near Childs Station, there is an extensive new citrus grove in which the orange trees are still less than 4 feet high. *A. humistrata* was absent, but *A. rolfsii* abounded and there were also a few plants of *A. tomentosa*. In undisturbed areas bordering the grove, the climax vegetation is largely scrub, in



FIG. 1. Four breeding areas of Monarch and Queen butterflies in south central Florida. See text for precise locations.

which *A. rolfsii* occurs quite commonly. The harrowing operations of the citrus companies appear not to be detrimental to *A. rolfsii*, but rather actually spread the plant vegetatively by dividing and distributing its large tuberous root.

A few miles south of Lake Childs, the sand ridge of central Florida ends and the scrub gives way to pine flatwoods which are largely slash pine (*Pinus palustris* Mill) and palmetto (*Sabal palmetto* (Walt.) Todd). Along the border of a stream in this vegetation type near the town of Old Venus, about 11 miles south of Area No. 2, a 5th species of milkweed was found, *Asclepias curassavica* L. (Area No. 3, Lat. 27° 4' 20" N; Long. 81° 22' 11" E.). This species is not native to North America (Woodson 1954). Collections were made on 4 individuals of this plant on January 1st 1959 by Dr. Stuart Frost of Pennsylvania State University and by us in March 1959.

About 55 miles south-southeast of Old Venus, at the junction of Florida highways 846 and 833 in Hendry County, collections were made on a 6th milkweed, *Asclepias incarnata incarnata* L. (Area No. 4, Lat. 26° 27' 30" N; Long. 81° 6' 21" E.). This plant was found growing abundantly in the marshes along the edge of the highway in this area which is in the north central part of the everglades-cypress country. We discovered the presence of breeding Monarchs and Queens here on June 17th, 1959 and subsequently made collections on the 27th of June and the 9th and 27th of July.

COLLECTING METHODS

At the beginning of this study in 1956, records of adult Monarchs and Queens from Area No. 1 included individuals which were netted and kept as well as those which were only observed. For this reason, the sexes of the butterflies are not recorded for that year. In 1959, the collecting techniques were refined and the adult records for Area No. 1 include only those that were captured and kept, or captured, marked, and released. In this way it was possible to avoid counting the same individual more than once and in addition the sexes were recorded. Recaptures are not included in these data.

Eggs and larvae of all instars were collected on the various species of milkweed by 2 persons systematically searching all the plants that could be found within a set period of time, usually about 2 hours, or 4 hours when only one person was present. Both the under and upper surfaces of all the leaves of each plant were searched, as well as the individual florets of each inflorescence. This thoroughness was necessary because the

female butterflies lay their eggs on both surfaces of the leaves, on the buds, on the pedicels, and occasionally on the plant stems. When eggs or larvae were found, they were permanently removed from the populations with part or all of the leaf or flower upon which they occurred and put into one half pint plastic snap-cap containers. Eggs and larvae were kept in separate containers, for, as noted elsewhere, the young instar larvae of both species are very prone to egg cannibalism (Brower ms. in prep.)

Larvae were easily identified by observing whether there was a pair of fleshy tubercles on the dorsum of the 2nd thoracic segment only (*D. plexippus*) or on the dorsum of both this and the 2nd abdominal segment (*D. g. berenice*). The instar of each larva was noted as it was collected. Eggs were brought back to the laboratory and redistributed so as to have only 2 per half pint container to reduce the chance of egg cannibalism by the first hatching larvae. They were checked daily up to 96 hours as it was found that hatching can occur any time up to 72 hours. A low proportion of eggs failed to hatch for unknown reasons.

OVIPOSITION BEHAVIOR OF FEMALES

The analysis of the data in this paper assumes that each egg on a plant is independent of others that may be found with it, that is to say, it is assumed that the females of both species tend to scatter their eggs rather than to lay them in clusters. This has been held to be so by previous investigators (e.g. Fisher 1930), and is supported by our field observations. We found that the foodplant searching pattern of the Monarch and Queen is an erratic, more or less random one in which the female repeatedly flutters down and establishes tarsal contact with the plants of the ground herb layer without any apparent selectivity but occasionally finds an *Asclepias* plant upon which it then lays an egg. After laying, it would fly up from the plant and resume its random search pattern. The chance that she would lay a 2nd egg on the same plant appeared no greater than it had been just prior to the initial discovery of the foodplant. However, in the course of collecting eggs, we found that young blossoming plants were far more likely to have eggs on them than either young or old plants which were not in bloom. Why this is so was suggested by our observations that the probability of a female discovering a foodplant was much greater if it were in bloom, the blossom serving as a medium-distance visual stimulus of an apparently *Asclepias*-specific nature. Now under

these conditions, even though the eggs are laid singly, the probability of laying a second egg on the same plant is increased because the female is more apt to be attracted back to the same plant than to non-blossoming ones in its immediate vicinity.

Another factor which probably contributes to the laying of more than one egg per plant is the elapsed time between successive ovipositions. If this time were great, motivation for laying would have greatly increased and the discovery of the foodplant might well result in more than one egg being laid.

When one considers the validity of the data then, it is important to realize that the egg collections in all but Area No. 3 were made where the milkweed plants were in abundance. This being so, the problem of egg concentration on any one plant by an individual ovipositing female is greatly reduced, and the assumption that each egg is laid independently seems justified.

RESULTS

Area No. 1

Table I summarizes the numbers of adult Monarchs and Queens collected in Area No. 1 during the spring and summer of 1956 and 1959. The results of the 2 years were put in a single chronological table because the trends in 1956 and 1959 are quite similar. The numbers for the 2 years are tabulated separately in detail in Tables III and IV.

TABLE I. Summary of adult frequencies for *Danaus plexippus* (Monarchs) and *D. berenice* (Queens) in Area No. 1, Highlands Co., Florida in 1956 and 1959

	March '59 (25-31)	April '56 (31 Mar.- 1 May)	May '56 (14-31)	Early June '56 (13-14)	Late June '59 (15-30)	July- August '59 (7 Jul.- 4 Aug.)
Monarchs. . .	23 (.28)	19 (.22)	4 (.05)	2 (.06)	1 (.02)	1 (.008)
Queens.	60 (.72)	68 (.78)	72 (.95)	29 (.94)	52 (.98)	122 (.992)
Totals. . . .	83	87	76	31	53	123

It can be seen in Table I that while the adult Monarchs comprise over one fourth of the combined populations of both species early in the spring, its frequency drops in May and June and becomes very much lower in July. Thus although the Queen adults always outnumber the Monarchs, the data are consistent with the hypothesis that the Monarchs migrate away from the wintering grounds as summer approaches.

As summarized in Table II, and tabulated in full in tables III and IV, data are presented

which establish for the first time that the Monarch breeds extensively in southern Florida which heretofore has been thought to serve only as an overwintering area (Williams 1930, 1938, 1958; Williams *et al.* 1942). The pattern of decreasing frequency of eggs and larvae as the summer approaches is similar to that found in the adults but, as can be seen from the data, the sudden drop occurs slightly later in the season, about mid June.

TABLE II. Summary of egg and larval frequencies for Monarchs and Queens on *Asclepias humistrata* and *A. rolfsii* in Area No. 1, Highlands Co., Florida, in 1956 and 1959

	March '59 (25-31)	April '56 (2-30)	Early June '56 (13-14)	Late June '59 (15-30)	July-August '59 (7 Jul-4 Aug)
Monarchs. . . .	344 (.93)	123 (.79)	48 (.61)	17 (.16)	1 (.003)
Queens.	25 (.07)	32 (.21)	31 (.39)	88 (.84)	337 (.997)
Totals.	369	155	79	105	338

TABLE III. Monarchs and Queens collected or observed in Area No. 1, Highlands Co., Florida, 1956

Adults	March	April										May				June					
	31	2	5	12	16	19	21	23	30			1	14	16	17	27	30	31	13	14	
Monarchs.	3	4	4	0	1	1	4	0	1			1	1	0	1	1	1	0		1	1
Queens...	10	10	4	3	5	4	12	5	5			10	9	12	10	12	14	15		17	12

Eggs and Larvae	April										June	
	2	5	7	9	15	16	19	23	26	30	13	14
Monarchs...	37	25	20	8	3	17	2	0	1	5	29	19
On <i>A. humistrata</i>												
Queens.....	3	4	4	3	0	0	7	3	2	1	8	5
Monarchs...	—	—	—	—	1	0	2	—	—	2	0	0
On <i>A. rolfsii</i> *												
Queens.....	—	—	—	—	1	1	2	—	—	1	9	9

* Dash indicates no collections made.

Moreover, in 1959 on the 15th and 16th of June, a higher proportion of the immature stages of the Monarchs were older than those of the Queens which suggests that they are the last major generation produced by the adult Monarchs before their nearly complete exodus from Florida. Of the 15 Monarchs found on these 2 days, 5 were found as 3rd instar larvae, 3 as 2nd instar, 2 as first, and only 5 as eggs. This contrasts with the 20 Queens of the same dates, 13 of which were found as eggs and the remaining 7 as 1st instar larvae. (A comparison of eggs *vs.* larvae found for the 2 species in a 2 x 2 contingency table gives a chi-square value of 3.41 which approaches significance at the .05 level).

TABLE IV. Monarchs and Queens collected in Area No. 1, Highlands Co., Florida, 1959

Adults	March* 25-31	June 15-16 22 30			July 7-8 15 18 22 28				August 4
Monarch ♂♂.....	11	0	0	0	0	0	0	0	0
Monarch ♀♀.....	12	1	0	0	1	0	0	0	0
Queen ♂♂.....	54	24	5	9	28	14	11	8	16
Queen ♀♀.....	6	8	2	4	13	2	2	2	7
Eggs and Larvae									
Monarchs...	344	15	1	1	1	0	0	0	0
On <i>A. humistrata</i> Queens.....	6	18	9	54	39	24	66	31	30
Monarchs...	0	0	0	0	0	0	0	0	0
On <i>A. rolfsii</i> Queens.....	19	2	1	4	3	17	16	19	38

* Adults not collected on 29 March, immatures not collected on 28, 29, or 30 March.

These egg and larval data are important from another point of view because they show that in the spring the Monarchs are reproducing at a much greater rate than the Queens present in the same area. Thus in the last week of March 1959, the Monarch adults represented only 28% of the combined adult population of Monarchs and Queens but at the same time their eggs and larvae represented 93% of the combined populations of offspring (Tables I and II). A possible interpretation of this is that the presence of the Monarchs has an inhibitory effect on the ovipositing Queen females. This hypothesis is supported by the data which strongly suggest that the Queen is more selective in its choice of foodplant species when the Monarchs are abundant in the spring than when they are rare in the summer (Table

TABLE V. Distribution of Queen eggs and larvae on *Asclepias humistrata* and *A. rolfsii* during spring and summer of 1959 showing that Queen females tend to avoid *A. humistrata* in spring (when Monarchs are common) but not in summer (when Monarchs are rare)

	25-31 March	15 June-4 August	Totals
On <i>A. humistrata</i> ...	6	296	302
On <i>A. rolfsii</i>	19	129	148
Totals.....	25	425	450

Chi-square = 22.3; d.f. = 1; $P < .001$.

V). Thus, in the spring the Queen females appear to avoid *Asclepias humistrata* and seek out *A. rolfsii*, whereas in the summer after most of the Monarchs have left, they lay their eggs freely on both plants. This interpretation is supported further by a consideration of the growth sequence of the 2 milkweeds as observed

by us in 1956 and 1959. *A. humistrata* has its peak in the spring and as the summer advances the plants begin to dry up, whereas *A. rolfsii* has its peak later in the season and lasts further on into the summer. Now as mentioned above, ovipositing females are highly attracted to the blossoms of both these milkweeds and *A. rolfsii* was just beginning to come into blossom in March when *A. humistrata* was at its maximum. We would therefore have expected on this basis alone that at this time the Queen females would have laid more eggs on *A. humistrata* than on *A. rolfsii*. This they did not do. It is therefore concluded that the Queen is displaced by the Monarch to a considerable extent during the spring when the Monarch is present in large numbers.

In order to be sure that the avoidance of *A. humistrata* by the Queen adults was not related to an inability of their larvae to eat it, we carried out the following preliminary foodplant experiment. Four females collected in Area No. 1 on June 30th 1959 were placed in an oviposition cage, described elsewhere (Brower *loc. cit.*), over *A. rolfsii*. After 53 hours, the eggs were collected by removing the leaves and flowers from the plants and brought back to the laboratory at the Archbold Biological Station. Here 80 were cut from the leaves on approximate 1 mm squares or left on the flower petals or buds. Forty of these were placed by two's in half pint plastic containers on half a leaf of *A. humistrata* and the remainder were similarly placed in containers with 3 leaves of the smaller *A. rolfsii*, so that the areas of leaves were about equal.

The resulting larvae were fed daily or every other day at which time their containers were cleaned and fresh food was added. When the larvae attained the 5th instar, they were transferred to one quart plastic containers in densities of 5. The rearing was carried out at room temperature between July 3rd and 22nd 1959. The results indicated that *A. humistrata* is at least as favorable for Queen larvae as *A. rolfsii* since 16 of 40 survived to produce adults on the former and 5 of 40 on the latter.

A second line of evidence suggesting that the species are interacting with one another is that the great reduction in larvae and eggs of the Monarch in June coincides with a build up in numbers of those of the Queen. Thus in 1959 on the 15th and 16th of June, 15 Monarchs were found, while in collections made on 2 days during the last 2 weeks of June they dropped to only 2. Conversely, the Queen was represented by 20 at the earlier dates and rose to 68 at the 2 later dates (Table IV). A comparison of the early *vs.* later

dates for the 2 species in a 2 x 2 contingency table shows that the observed differences are highly significant ($\chi^2 = 27.3$, $P < .001$).

Areas Nos. 2, 3, and 4

In Table VI, data are presented for egg and larval collections made on *A. rolfsii* in Area No. 2. Except for July 2nd and 18th, the records were occasional ones gathered while picking food-plants or collecting the common Queen adults for laboratory purposes. Nevertheless, it can be seen that immature Monarchs were present as late as August 5th. In addition, one adult male was caught on July 10th and single adults of undetermined sex were observed on July 11th and August 1st and 7th. It is thus clear that the Monarch, although in low frequency, maintains a breeding population at least through July in south central Florida.

TABLE VI. Occasional records of eggs and larvae of Monarchs and Queens on *Asclepias rolfsii* in Area No. 2, Highlands Co., Florida, in 1959

	DATES OF COLLECTION							
	31 March	29 June	2 July	3 July	7 July	17 July	18 July	5 August
Monarchs.....	4	0	6	2	0	1	0	1
Queens.....	6	7	41	12	8	—*	16	—

* Dash indicates collections not made.

While these findings indicate how late into the summer Monarchs breed in this region, observations made by Dr. S. Frost in Area No. 3 indicate that they also breed here in mid winter. According to him, 4 Monarch and 2 Queen 2nd or 3rd instar larvae were present on *Asclepias curassavica* on January 1st 1959. We visited the same area again on March 28th and found 28 eggs and larvae of the Queen, but none of the Monarch. No attempt was made to collect adults in this area.

Other evidence that the Monarch breeds in its eastern overwintering range was discovered in Area No. 4 (Table VII). Extensive collections were made here in 1959 on June 27th, July 9th and 27th. Two Monarch adults were caught on the June date and an additional one seen, but no eggs or larvae were found at that time. On the 9th of July, this situation was reversed; no adult Monarchs were present, although 32 eggs were found on the *Asclepias incarnata* plants. On July 27th, neither eggs nor adult Monarchs were present. It seems likely that the sporadic occurrence of the Monarch in this area reflects its low summer population density, there being a total

of 199 Queen adults to 2 Monarch adults collected on all 3 dates. Moreover, all the immature Monarchs were found as eggs, whereas the Queen always was represented by eggs and larvae of all instars except in June when all but 5th instar larvae were there.

TABLE VII. Monarchs and Queens collected in Area No. 4, Hendry Co., Florida, 1959

Adults	27 June*	9 July	27 July
Monarch ♂♂.....	1	0	0
Monarch ♀♀.....	1	0	0
Queen ♂♂.....	64	27	15
Queen ♀♀.....	50	10	23
Eggs and larvae on <i>Asclepias incarnata</i>			
Monarchs.....	0	32	0
Queens.....	126	76	70

* One additional Monarch adult seen but not caught.

DISCUSSION

Breeding in overwintering areas

Until the present time, it has been emphatically held that the Monarch does not reproduce in the areas where it overwinters (Williams 1958)¹. The support for this view was obtained largely by studying the spectacular overwintering populations that occur each year on the coast of California. Here Downes (in Williams *et al.* 1942) found that, although some individuals were active, both feeding at flowers and copulating, egg maturation did not occur in most cases until the spring when the groups began breaking up. It appears that the coastal areas are unsuitable for the larval foodplants and that the areas inland where these are more abundant are not favorable for the Monarch during the cold part of the year.

In contrast to the overwintering populations in the western part of the range of the Monarch, all that is known about them in the east is that they form winter congregations in several places in Florida. To this date no conclusive evidence has been presented to indicate whether or not breeding occurs in this area. However, the data presented in this paper establish that the Monarch butterfly does in fact breed extensively in the

¹ Urguhart (1960) in his recent book published while this manuscript was in press, limits the breeding range of the Monarch roughly between latitudes 32° N. and 48° N. (p. 298), thus agreeing with Williams. This statement is made notwithstanding new findings to the contrary which are cited (p. 174) but minimized in his conclusions (p. 300).

central region of southern Florida from the latter part of March through the middle of June. Furthermore, breeding Monarchs were found in January in the same area, although no organized study has been made earlier than the March observations. And finally, breeding occurs at a low level at least through July in this general region. It is most probable that the Monarch continues to breed and maintains itself at very low numbers throughout the summer in this part of Florida, but more observations are needed to establish this. Although preliminary recapture data indicate that the Monarch adults linger in this area in the early spring (Brower ms. in prep.), several changes occur which are consistent with the hypothesis that the bulk of them move out of Florida as summer approaches. First of all, there is a drop in the frequency of adults. Second, this is followed by a decline in the frequency of eggs and larvae which finally drop off abruptly to a very low level after the middle of June. And third, just before this final drop, the age structure of the population of eggs and larvae differs from that of the vigorously breeding Queens in that the proportion of older larvae is much higher in the Monarch.

Significance of breeding in the overwintering area

It is of course possible that the adults produced by these breeding populations in southern Florida die without contributing to the migratory population. However, the massive extent to which they reproduce in the spring makes it seem far more likely that they do constitute a reservoir from which many Monarchs move northward and repopulate eastern North America. It thus seems probable that the northward movements of the Monarch butterfly in the east are performed partly by offspring of later generations of the Monarchs which flew south in the fall and partly by the overwintering individuals themselves. When more fully investigated, it may well be found that similar winter reproduction occurs in southern California, and also in Mexico where all we know is that the Monarchs fly southward in the fall. In support of this prediction are the unusual individuals which Downes recorded as reproducing in the winter in southern California. Should winter breeding occur in all these areas, and, if it can in fact be shown that the offspring migrate northward, then the periodic movements of the Monarch would have to be reclassified as partly remigration rather than solely a form of true migration that it has been held to be to date. It is even possible that none of the fall migrants returns to the north, those that do being instead

their offspring bred in the vicinity of the overwintering areas. Should this prove to be so, then the Monarch butterfly would not be a true migrant species at all.

Ecological interaction of Monarch and Queen

When one considers the very great development of foodplant specificity in the Lepidoptera, it is a striking fact that 2 species as large as the Monarch and Queen share the same larval foodplants. That they do is even more unusual since the Florida *Asclepias* species upon which we found the immature stages of both are not large plants and deteriorate rather rapidly after blooming. Moreover, they are neither common, nor do they frequently occur together in great clumps. These facts suggest that food shortage is a possible limiting factor for the butterflies and, although we have no quantitative data at present, those plants upon which we discovered full grown larvae were very often seriously defoliated. Not only do the larvae eat the same plants, but the adults of both species are highly attracted to the blossoms of the milkweeds where they obtain nectar. It is thus clear that the Monarch and Queen are ecologically very similar species, and it is an extremely suggestive fact that one is migratory while the other is not, being limited throughout the year to the southern part of the United States and southward in the form of 2 subspecies from east to west (Klots 1951). It is possible to ask the question, has the origin of migration of one of the species been favored by natural selection as a type of "character displacement" (Brown and Wilson 1956, Brown 1958), so often found in closely related species of animals? Here the migration would result in the lessening of ecological competition which comes about through sharing the same foodplants.

Two aspects of this study of the breeding populations in southern Florida suggest that ecological competition occurs between these 2 butterflies. First, there is the reduction in the numbers of eggs and larvae of the Monarch in June which coincides with an increase in those of the Queen. And second, there is the extraordinary fact that in the spring when the Monarchs are breeding profusely, the Queen females for the most part avoid the most common *Asclepias* species on which they later readily oviposit after the Monarchs have left.

It is planned to study the interactions of these species further in their natural environment and also in laboratory and outdoor cage experiments. They present a rare opportunity to observe the actual occurrence of competition in nature be-

tween species at the same trophic level for which there exists so much indirect evidence but so little direct evidence, as emphasized by Elton and Miller (1954), Hutchinson (1957), Brower (1959), and Hairston (1959).

SUMMARY

1. Data are presented which for the first time indicate that the Monarch butterfly (*Danaus plexippus*) breeds extensively in its eastern overwintering range in south central Florida.

2. As a result of this discovery, the Monarch may prove not to be a truly migrant species, but rather one exhibiting the phenomenon of remigration.

3. As the summer approaches, several changes occur which are consistent with the hypothesis that the breeding populations contribute to the northward movement of the species: the frequency of adults drops, followed by a similar decline of eggs and larvae, and just before almost completely disappearing, the population structure of the immature stages contains a higher proportion of older individuals.

4. Breeding of the Monarch occurs in this area in January and a small population probably continues to breed throughout the summer. More data are needed on both these points.

5. It is suggested that the origin of migration in the Monarch butterfly may be related to competition with the ecologically very similar species *Danaus gilippus berenice*, the Queen, which does not migrate and is limited in distribution to the southern part of the United States and southward.

6. Evidences of competition are several: adults of both species are highly attracted to the flowers of the same milkweed plants (*Asclepias* spp.) upon which they both feed and lay their eggs and on which their larvae feed; the Queen females tend to avoid one species of milkweed when the Monarchs are present, but then readily oviposit on it after the Monarchs have flown northward; and the disappearance of the Monarch coincides with an increase in the population size of the Queen.

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A STUDY OF BENTHIC FAUNA IN A RECENTLY CONSTRUCTED BOAT HARBOR IN SOUTHERN CALIFORNIA¹

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INTRODUCTION

The study of succession in the marine environment has been difficult because of inability to start from the beginning. Much of the work has been concerned with the settlement of fouling organisms on test panels (Anon 1952) or on an intertidal rock face following removal of the attached organisms (Hewatt 1935). In these studies it was found that some of the earliest inhabitants are essential for seating of some of the later animals, and that some of the earlier species drop out during the development of the climax condition.

The few studies concerned with succession in the subtidal realm have been associated with the development of public works. Brandt (1897) collected the animals that had settled on the bottom of Kiel Canal a few months after it was constructed connecting the North and Baltic Seas. In this short period of time he found 5 species of invertebrates distributed throughout nearly the 100 kilometer length of the canal. These were the crustaceans *Balanus improvisus*, *Gammarus locusta*, and *Mysis vulgaris*; the polychaete *Polydora ciliata*; and the bryozoan *Membranipora pilosa*. Additional groups of species were limited to one end of the canal. The author (1956, 1957) studied the animals that had settled on the bottom near the mouth of the San Gabriel River and a portion of the Los Angeles Harbor after they had been dredged. Both of these areas were heavily polluted and essentially devoid of marine organisms prior to dredging. Dredging activity removed the pollutants from the bottom, but the subsequent accumulation of toxic materials reduced the bottom population to its former levels 1.5 years later.

Shelford, *et al.* (1935) described the bottom communities in Puget Sound, Washington. They concluded that succession took place rapidly in the sea with the climax community on hard bottoms being reached within a year or two. They believed that succession was less rapid on the soft bottom because the establishment of a hard bottom community on a comparatively soft bottom must await the accumulation of shells.

In 1955 the City of Long Beach let a contract for dredging and construction of a boat harbor adjacent to Alamitos Bay (Figure 1). This area had not been previously exposed to sea water and offered a unique opportunity to study succession in a subtidal marine area from the beginning. This paper describes the results of quantitative benthic studies in the first basin of the boat harbor from 1956 to 1959. The quantitative distribution of the benthic invertebrates had been studied previously in the other portions of Alamitos Bay by Reish and Winter (1954).

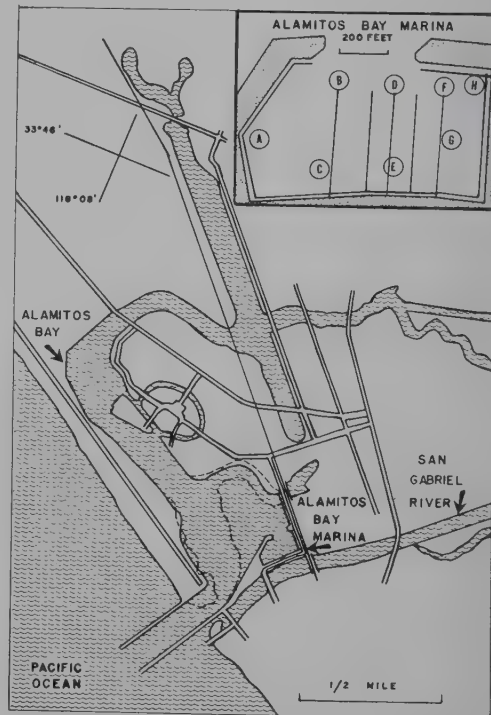


FIG. 1. Map of Alamitos Bay, California. Dotted lines indicate former boundaries before construction of marina. The station locations in the marina are represented in the inset.

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assistance in the field work. The amphipod crustaceans were identified by Dr. J. Laurens Barnard. Some of the molluscs were identified by Dr. Norman Mattox and Mr. Gilbert F. Jones.

DESCRIPTION OF ALAMITOS BAY MARINA

The entrance to Alamitos Bay (Fig. 1) is located in the City of Long Beach at the southeastern boundary of Los Angeles County, California. The bay is used primarily as a recreational area for swimming, sun-bathing and boating. The early history and development of the area has been described previously (Reish and Winter 1954).

Alamitos Bay Marina is the first of a series of basins that are being constructed for boat moorages by the City of Long Beach. The present basin comprises an area of 12.45 acres (50,385 square meters). The marina was dredged from land to a depth of —12 feet mean low water. The former boundaries of Alamitos Bay in the vicinity of the marina are represented by dotted lines in Fig. 1. Dredging of the marina commenced in the fall of 1955. After completion of the bulkheads, sea water was admitted during the early part of 1956 into the basin and the central portion dredged to the required depth.

MATERIALS AND METHODS

The bottom samples were taken at 8 stations (Fig. 1) from floating docks with a size one Hayward orange-peel bucket (Reish 1959a). The sample was emptied into a tub, then transferred into gallon jars and preserved with full strength formalin. The amount of material taken in a single grab generally ranged from 3 to 4 liters. The material was screened in the laboratory using a mesh having 20 openings to the inch. The animals were separated from the other material retained on the screen and identified. Samples were taken on May 15 and November 29, 1956; April 24 and December 7, 1957; April 26 and August 6, 1958; and August 5, 1959.

CHEMICAL AND PHYSICAL CHARACTERISTICS

The substrate is uniform throughout the basin; it consists primarily of gray clay with small fragments of mica. Black sulfide mud was first encountered at Station D during the November 1956 survey and at Station H in April 1957. All stations had black sulfide mud in August 1958 and 1959. Cores taken with a portable piston corer (Reish and Green 1958) at Stations D and E in 1958 showed an upper layer from 5 to 8 cm thick of black sulfide mud overlying gray substrate.

The organic carbon content of the substrate was determined for April and December 1957, and for April and August 1958, utilizing the potassium dichromate method as applied to marine sediments by Emery and Rittenberg (1952). The values for organic carbon ranged from 0.4 to 1.6% with the majority of the determinations at about 1.0%. Slightly higher values were encountered at the outer stations (B, D, and F) than at the inner stations (C, E, and G); however, the difference is small and may not be of significance.

Water temperatures at the surface and at the 15 foot depth and dissolved oxygen determinations (Standard Methods) of the water mass at the 15 foot depth have been taken monthly from May 1956 through August 1959 at Station D. Surface temperatures ranged from 13.5° C to 25.0° C with a median of 20.5° C. The temperature at the 15 foot depth ranged from 13.2° C to 25.0° C with a median of 19.5° C. The higher temperatures were encountered during June and July 1959, and the colder waters measured in February 1957.

The dissolved oxygen content of the water mass at the 15 foot depth ranged from 2.6 to 8.9 with a median of 6.1 ppm. Dissolved oxygen determinations were made at Stations D and E in August 1958 and August 1959 at intervals of 3 feet from the surface to near the bottom where the interval was one foot. Little variation in the amount of dissolved oxygen at different depths was noted except at Station E in August 1958. Here the amount of oxygen was only 1.2 ppm at 6 inches above the bottom as compared to 3.7 ppm in the water above.

RESULTS

During the course of the seven benthic surveys, 3,186 specimens representing 94 species were collected. The species are listed together with the number of individuals taken at each survey in Table I. The data for the 8 stations of each survey have been totaled together. The polychaetous annelids constituted the most important animal group collected; 60% of the species and 87% of the specimens were polychaetes. Mollusca, particularly pelecypods, comprised 19% of the species but only 3% of the specimens. Similarly, 16% of the species were crustaceans but only 2% of the specimens. Unidentified nemerteans were represented by 177 specimens or 6% of the total.

The polychaetous annelids were always the dominant group of organisms. Only in August 1958 did the number of polychaete species fall be-

TABLE I. List of species and number of specimens collected from the bottom of Alamitos Bay Marina May 1956 through August 1959

	5/56	11/56	4/57	12/57	4/58	8/58	8/59	Totals
Phylum Platyhelminthes								
Turbellarians, unidentified	4	—	—	1	—	—	—	5
Phylum Nemertea								
Nemerteans, unidentified	49	25	47	43	1	9	3	177
Phylum Annelida								
Class Polychaeta								
<i>Harmothoe lunulata</i> (delle Chiaje)	5	—	—	—	4	—	1	10
Polynoids, unidentified	—	—	1	1	—	—	—	2
<i>Anatides williamsi</i> Hartman	1	—	—	—	—	—	—	1
<i>Eteone dilatata</i> Hartman	1	3	3	2	1	—	—	10
<i>Eumida sanguinea</i> (Oersted)	—	—	5	—	—	—	—	5
Phyllodocids, unidentified	—	—	5	—	—	—	—	5
<i>Ancistrosyllis bassi</i> Hartman	—	—	1	—	—	—	1	2
<i>Leocrates</i> sp.	—	1	—	—	—	—	—	1
<i>Podarke pugettensis</i> Johnson	2	1	3	1	—	1	—	8
<i>Neanthes</i> sp.	1	—	—	—	—	—	—	1
<i>Nereis neongripes</i> Hartman	—	—	3	—	—	—	—	3
<i>N. procerata</i> Ehlers	—	1	—	—	—	—	—	1
<i>Platynereis bicanaliculata</i> (Baird)	1	1	1	—	1	—	—	4
<i>Nephtys caecoides</i> Hartman	3	—	7	—	—	—	—	10
<i>Glycera americana</i> Leidy	—	1	—	1	1	—	—	3
<i>Goniada littorea</i> Hartman	—	—	1	1	1	—	—	3
<i>Diopatra splendidissima</i> Kinberg	3	12	1	—	1	—	1	18
<i>Lumbrineris erecta</i> (Moore)	5	4	10	31	22	11	43	126
<i>L. minima</i> Hartman	28	134	152	94	105	74	57	644
<i>Dorvillea articulata</i> (Hartman)	9	58	280	33	11	—	24	415
<i>Haploscoloplos elongatus</i> (Johnson)	18	44	43	41	32	—	44	222
<i>Paraonis g. oculata</i> Hartman	—	1	—	—	—	—	—	1
<i>Laonice cirrata</i> (Sars)	1	—	—	—	1	—	—	2
<i>Nerinides acuta</i> (Treadwell)	—	—	—	9	—	—	—	9
<i>Polydora</i> (B.) <i>uncata</i> Berkeley	—	—	—	—	—	—	1	1
<i>P. (C.) paucibranchiata</i> Okuda	—	—	—	—	1	—	—	1
<i>P. socialis</i> Schmarda	—	—	—	—	1	—	—	1
<i>P. sp.</i>	—	2	2	2	—	—	—	6
<i>Prionospio cirrifera</i> Wiren	—	9	86	60	22	35	5	217
<i>P. h. newportensis</i> Reish	1	5	12	8	1	—	4	31
<i>P. pinnata</i> Ehlers	1	3	4	—	3	—	—	11
<i>Spiophanes missioniensis</i> Hartman	1	7	10	8	29	—	—	55
<i>S. pigmentata</i> Reish	1	2	7	7	8	—	—	25
<i>Streblospio benedicti</i> Webster	—	2	1	—	—	—	1	4
Spionids, unidentified	—	3	2	1	—	—	—	6
<i>Spiochaetopterus</i> sp.	—	1	7	2	—	1	—	11
<i>Chaetozona corona</i> Berkeley	2	2	2	1	5	—	—	12
<i>Cirrifornia luxuriosa</i> (Moore)	—	—	—	—	—	—	6	6
<i>C. spirabranchia</i> (Moore)	3	—	—	—	—	—	—	3
<i>Cossura candida</i> Hartman	—	—	—	2	3	—	1	6
<i>Tharyx multifilis</i> Moore	—	—	—	—	3	—	—	3
<i>T. parvus</i> Berkeley	1	21	16	5	7	5	—	55
<i>Pherusa capitata</i> (Moore)	4	1	2	9	4	—	1	21
<i>Armandia bioculata</i> Hartman	1	22	7	3	—	—	—	33
<i>Capitella capitata</i> (Fabricius)	—	—	—	1	—	—	2	3
<i>Capitella ambiseta</i> Hartman	70	75	111	41	50	5	7	359
Capitellid, unidentified	—	—	—	1	—	—	—	1
<i>Pectinaria californiensis</i> Hartman	13	15	18	—	—	—	—	46
<i>Asychis similis</i> (Moore)	1	—	—	—	—	—	—	1
<i>Amage anops</i> (Johnson)	—	—	—	—	1	—	—	1
<i>Ampharete arctica</i> Malmgren	—	—	3	—	2	—	—	5
<i>Amphicteis scaphobranchiata</i> Moore	14	5	20	2	—	—	—	41
<i>Amatea occidentalis</i> Hartman	8	5	22	3	40	—	5	83
<i>Pista alata</i> Moore	17	8	9	4	11	—	7	56

TABLE I. (Continued)

	5/56	11/56	4/57	12/57	4/58	8/58	8/59	Totals
<i>Euchone</i> sp.....	—	—	109	7	11	—	—	127
<i>Megalomma</i> sp.....	11	7	1	—	—	—	—	19
Phylum Arthropoda								
Class Crustacea								
<i>Amplisca cristata</i> Holmes.....	—	—	3	—	—	—	—	3
<i>Amphideutopus oculatus</i> Barnard.....	—	—	2	—	—	—	—	2
Aorid, unidentified.....	—	—	—	—	—	1	—	1
<i>Corophium acherusicum</i> Costa.....	—	—	—	—	—	—	2	2
<i>Corophium</i> sp.....	—	1	—	—	—	—	—	1
<i>Elasmopus rapax</i> Costa.....	—	1	—	—	—	—	—	1
Amphipods, unidentified.....	1	1	—	1	—	—	—	3
<i>Metacaprella</i> sp.....	1	4	—	—	1	—	—	6
<i>Livoneca</i> sp.....	—	—	—	—	—	1	—	1
Isopod, unidentified.....	—	—	—	—	1	—	—	1
<i>Callinassa californiensis</i> Dana.....	—	1	2	3	10	9	5	30
<i>Crangon californiensis</i> (Holmes).....	—	—	—	5	—	—	5	10
Shrimp, unidentified.....	—	1	8	2	1	—	1	13
<i>Hemigrapsus oregoniensis</i> (Dana).....	—	—	—	—	—	—	1	1
<i>Pinnixa franciscana</i> Rathburn.....	2	—	1	1	2	1	—	7
Class Pycnogonida								
Pycnogonid, unidentified.....	1	—	—	—	—	—	—	1
Phylum Mollusca								
Class Pelecypoda								
<i>Chione undatellum</i> (Sowerby).....	—	3	2	—	—	—	—	5
? <i>Evilia</i> sp.....	1	—	—	—	—	—	—	1
<i>Laevicardium substriatum</i> (Conrad).....	—	2	—	—	—	—	1	3
<i>Lysonia californica</i> Conrad.....	2	—	1	—	—	—	—	3
<i>Macoma nasuta</i> (Conrad).....	4	18	1	21	3	2	2	51
<i>Mytilus edulis</i> Linnaeus.....	—	—	—	—	1	—	—	1
<i>Rochefortia</i> sp.....	—	10	—	—	—	—	—	10
<i>Saxidomus nuttalli</i> Conrad.....	—	—	—	—	—	1	—	1
<i>Tagelus californica</i> Conrad.....	—	2	—	2	—	—	1	5
<i>Tellina butoni</i> Dall.....	—	—	—	1	1	—	—	2
<i>T. carpenteri</i> Dall.....	—	1	2	—	—	—	—	3
Clam A, unidentified.....	—	—	1	4	3	—	1	9
Clam B, unidentified.....	—	—	—	—	1	—	—	1
Class Gastropoda								
<i>Acteonina smira</i> Dall.....	—	—	1	—	—	—	—	1
<i>Bullaria gouldiana</i> (Pilsbry).....	—	—	—	10	—	—	—	10
<i>Crepidula onyx</i> Sowerby.....	—	—	—	1	—	—	—	1
<i>Nassarius mendicus</i> (Gould).....	—	—	—	—	—	—	1	1
Tectibranchs, juvenile.....	4	—	1	—	—	—	—	5
Phylum Phoronidea								
Phoronids, unidentified.....	10	6	1	5	1	2	—	25
Phylum Echinodermata								
Class Holothuroidea								
<i>Leptosynapta albicans</i> (Selenka).....	27	—	—	—	—	—	—	27
Total number of species.....	41	45	50	43	41	15	29	94
Total number of specimens.....	333	532	1040	481	408	158	234	3186

low 50% of the total. At least 70% of the specimens counted in each survey were polychaetes. The relative importance of the crustaceans and molluscs in both numbers of species and specimens fluctuated with one another during the period of the study.

The number of species and specimens for each

survey is summarized in Figure 2. The data for all the stations of each survey were treated as a unit. Initially, 41 species were collected in May 1956, followed by a rise until April 1957 when 50 species were taken. A slight decrease in the number of species was noted the next 2 sampling periods. This was followed by a sharp decrease

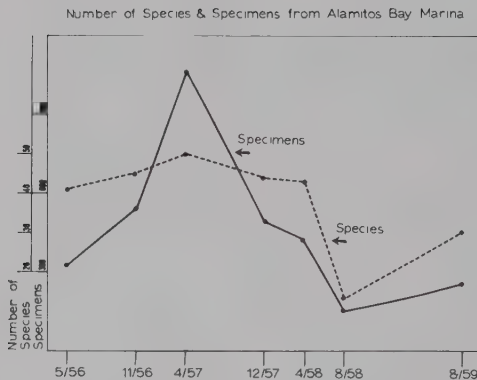


FIG. 2. Graphic representation of the number of species and specimens collected each survey from the Alamitos Bay Marina.

from April to August 1958. There was a slight increase in the ensuing year.

The curve for the number of specimens approximates that of the species but the magnitude is greater. The increase in the number of specimens was rapid with a peak of 1,040 counted in April 1957. Following this peak there was a sharp decrease in the number collected. Only 158 specimens were taken from the 8 stations in August 1958. There was a slight increase in the number of specimens in the August 1959 survey.

Occurrence of Principal Species

The occurrence and abundance of the principal bottom-dwelling species in Alamitos Bay Marina are summarized in Figure 3. It can be observed that some species were relatively constant; others fluctuated considerably; and still others appeared, then disappeared. A discussion of the species represented in Fig. 3 and some additional ones is given below.

Lumbrineris erecta (126 specimens) is one of the larger polychaetes collected. It lives in the substrate but does not maintain a burrow. Little variation in the number of specimens collected was noted through August 1958; the largest number of *L. erecta* was encountered in August 1959.

Lumbrineris minima (644) was the dominant organism in 5 of the 7 surveys. The greater number of individuals was collected in November 1956 and April 1957, which corresponded to the time of the peak in the total animal population (Figure 2). This polychaete is a slender, elongated worm with habits similar to *L. erecta*.

Dorvillea articulata (415) was present in all but the August 1958 survey. The majority of the specimens were collected in April 1957 when 280

individuals were encountered. This species may either crawl on or burrow into the substrate.

Haploscoloplos elongatus (222) was present in about the same numbers during the period of study except in August 1958 when none was taken. The habits of this species are unknown.

Prionospio cirrifera (217) was not encountered until the 2nd survey; it reached its maximum numbers in April 1957, and has gradually declined since that time. This polychaete constructs mud tubes.

Spiophanes missioniensis (55) was never abundant at any one time nor was it found in large numbers from any one sample. It was not collected in the last 2 surveys. This species also builds tubes but it utilizes a larger grain size than *Prionospio cirrifera*.

Tharyx parvus (55) was found frequently but never abundantly. It was not taken in August 1959. This polychaete burrows into the substrate and extends its branchiae to the substrate-water interface.

Capitita ambiseta (359) was present in large numbers during the first surveys, but since April 1957 it has declined in numbers. It lives in the substrate but does not maintain a definite burrow.

Pectinaria californiensis (46) is a polychaete that constructs a cone shape tube from sand grains. A total of 46 specimens was collected from May 1956 through April 1957; it has not been taken since although empty tubes have been observed. This species burrows its anterior end into the substrate leaving its posterior end extending up.

Amaea occidentalis (83) is a large polychaete that constructs a mud tube. It was taken every time except in August 1958.

Euchone sp. (127) suddenly appeared in large numbers in April 1957 and then disappeared 2 periods later. This species builds a mud tube in the substrate.

Unidentified nemerteans (177) of perhaps more than one species were collected in similar numbers through December 1957 after which they declined in numbers.

Macoma nasuta (51) was the most frequently encountered molluscan. Small peaks in numbers of individuals were noted in November 1956 and again in December 1957. Nothing is known concerning the reproductive period of this pelecypod. *Macoma nasuta* burrows into the substrate and extends a siphon to the surface to feed.

Leptosynapta albicans (27), a holothurian, was the most conspicuous and largest species encountered in May 1956, but it has not been collected since. This species is known to inhabit

OCCURRENCE AND ABUNDANCE OF DOMINANT SPECIES

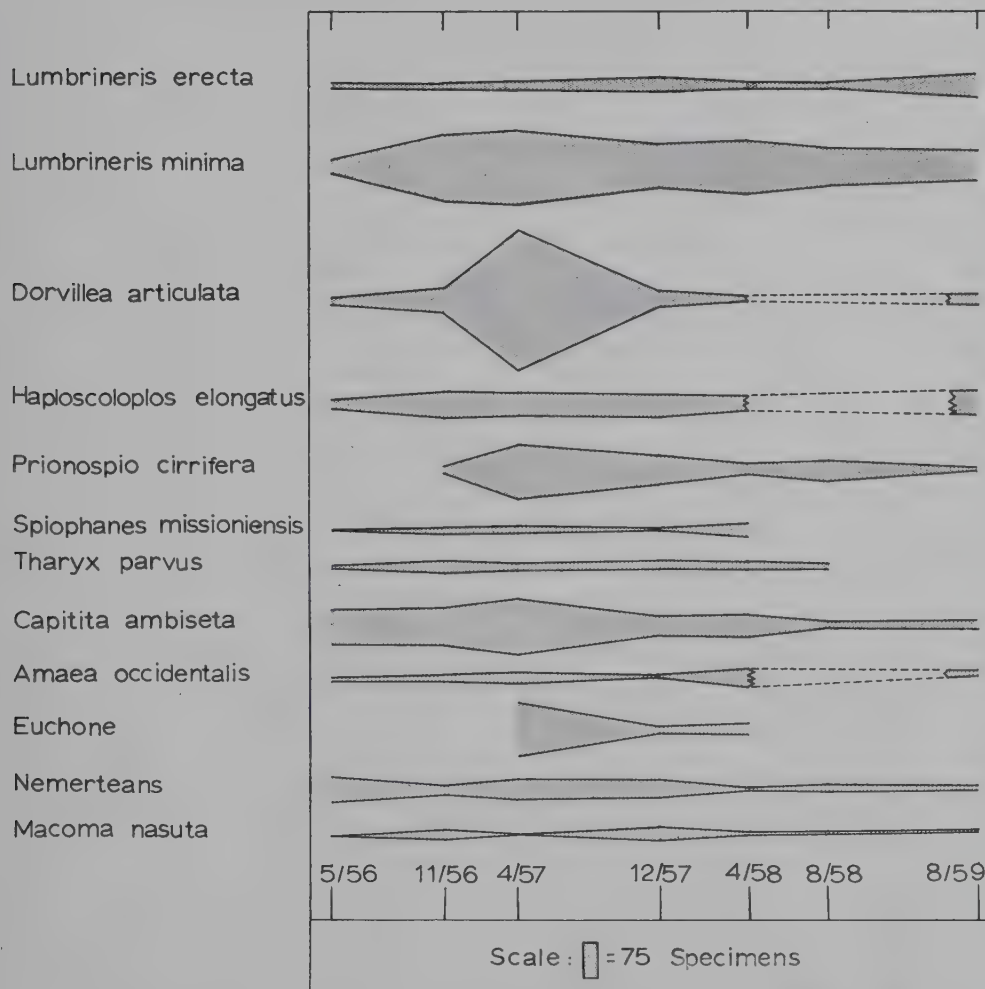


FIG. 3. Diagrammatic representation of the occurrence and abundance of the dominant species collected from the Alamitos Bay Marina.

sandy to muddy substrates and engulf the material for the contained detritus.

DISCUSSION

In order to determine whether or not succession has occurred in Alamitos Bay Marina, it is important to consider what constitutes the climax community in nearby areas with similar environmental conditions. The quantitative distribution of the benthic organisms in Alamitos Bay was studied before the construction of this boat harbor (Reish and Winter 1954). The benthic animals have been studied in nearby Los Angeles-Long Beach Harbors (Reish 1959c), and the poly-

chaetes in Newport Bay (Reish 1959b). The substrate typically consisted of gray mud at the outer reaches of these bays and harbors and in Alamitos Bay Marina. The temperature, chlorinity, and dissolved oxygen content of the water mass were similar at these areas. The polychaetous annelids were the dominant species of animals encountered in Alamitos Bay and Los Angeles-Long Beach Harbors. It can be seen from Table II that the climax community in the established areas studied consisted of *Lumbrineris minima*, *Cossura candida*, and *Capitita ambiseta*. This community may be modified in the different areas by the presence of additional species of

polychaetes, notably *Dorvillea articulata*, *Haploscoloplos elongatus*, and *Tharyx parvus*. Both *Lumbrineris minima* and *Capitita ambiseta* were found abundantly in the marina at the time of the first survey (Table I). *Cossura candida* has never been found abundantly in the marina.

TABLE II. Comparison of the distribution of the Dominant polychaete species in southern California bays and harbors with Alamitos Bay Marina

Species	Alamitos Bay	Alamitos Bay Marina	Los Angeles Long Beach Harbors	Newport Bay
<i>Nereis procera</i>	—	x	xx	x
<i>Lumbrineris erecta</i>	x	xx	x	xx
<i>L. minima</i>	xx	xx	xx	xx
<i>Dorvillea articulata</i>	x	xx	xx	xx
<i>Haploscoloplos elongatus</i>	xx	xx	xx	xx
<i>Prionospio cirrifera</i>	—	xx	x	x
<i>P. h. newportensis</i>	xx	x	x	xx
<i>Spiophanes missioniense</i>	x	xx	x	x
<i>Cossura candida</i>	xx	x	xx	xx
<i>Tharyx parvus</i>	x	xx	xx	xx
<i>Armandia bioculata</i>	x	x	x	xx
<i>Capitita ambiseta</i>	xx	xx	xx	xx

xx Dominant organism.
x Present.
— Absent.

It is of interest to consider what has been occurring with respect to time with the more important dominant polychaetes in Alamitos Bay Marina (Table I; Figure 3). The majority of these species have diminished in number in the recent samplings. Only *Lumbrineris erecta* and *Haploscoloplos elongatus* were found in increasing numbers at the time of the last survey.

There is no indication of succession in the newly constructed boat harbor. No sequence of species was noted during the course of the study. Of the dominant species listed for the marina in Table II, only *Prionospio cirrifera* was not collected at the time of the first survey; however, it was found in large numbers by November 1956. The species composition has remained relatively constant, with the variations discussed above, during these first 3 years of the marina; the number of specimens collected has varied considerably. Several possible explanations may be presented for the decrease in the population following the peak in April 1957. All the water that enters and leaves the boat basin passes through a single entrance (Figure 1). This limitation on water circulation may affect the bottom deposits after a period of time by a lack of a sufficient oxygen supply. Evidence for this may be that black mud possessing a sulfide odor was first observed No-

vember 1957 and was found at all stations in August 1958. Additional supporting data may be that on one occasion toward the end of the study low dissolved oxygen was encountered just above the bottom. Soundings were made throughout the marina and past the entrance to determine whether or not there was a sill present which could entrap the deeper water, such as occurs in the basins off southern California (Emery and Rittenberg 1952). No sill was encountered; the water depth increased from the basin to beyond the entrance. Boats were first moored in the marina in February 1957, and it is possible that pollution, either domestic or oil, may have been the cause of the reduction in the population. Local regulations restrict the discharge of pollutants into the marina, and visually there appears to be little or no evidence of such pollution. None of the species of polychaetes known to be indicators of pollution (Reish 1959c) was found in large numbers in the marina.

In the course of study, there was no evidence that a soft bottom community gives rise to a hard bottom community as proposed by Shelford, *et al.* (1935), for Puget Sound, Washington. While hard bottoms composed of shell fragments have been found at isolated stations in Los Angeles inner harbor (Reish 1959c), and Newport Bay (Barnard and Reish 1959), the majority of the substrates in the bays and harbors of southern California are composed of fine muds. Molluscs comprise only a small proportion of the bottom fauna in these areas, and the number of species and specimens did not vary appreciably during the 3 years.

SUMMARY

1. A periodic quantitative study was made in a newly dredged marine boat harbor to determine whether or not the subtidal benthic fauna succession occurred on the bottom.
2. Polychaetes comprised 60% of the species and 87% of the specimens collected. Molluscs, crustaceans, and nemerteans were the other important groups taken.
3. A peak in the number of species and specimens was reached about 2 years after sea water was first let in. The population decreased markedly in the ensuing year. Various explanations for this reduction in the number of species and specimens are discussed.
4. The principal bottom-dwelling species in Alamitos Bay Marina include 11 species of polychaetes, unidentified nemerteans, and one species of pelecypod. The occurrence, abun-

dance, and ecology of these species are discussed.

5. There was no evidence of succession in Alamitos Bay Marina. The principal species were dominant during the entire period of study. The bottom fauna was compared with the other portions of Alamitos Bay, Lower Newport Bay, and outer Los Angeles-Long Beach Harbors. In general, the faunas of all regions were similar. The polychaete *Cossura candida* was only encountered sparingly in the marina, but this species constitutes an important element of the benthic fauna in the other areas.

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TEMPERATURE RELATIONSHIPS IN A PINK SALMON STREAM IN ALASKA¹

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INTRODUCTION

The pink salmon (*Oncorhynchus gorbusha*) has a life cycle of 2 years. In southeast Alaska eggs are deposited in the gravels of coastal streams from July until October and fry migrate into saltwater the following spring. In the entire life history, it is during the freshwater stage of development that the heaviest mortalities occur as a result of changes in physical properties of the environment.

In 1948, under the direction of Dr. W. F. Thompson, an investigation was begun of factors which may affect freshwater survival of pink salmon² in southeast Alaska. The purpose of this work was to provide a basis for long-continued

observations of southeast Alaska streams to correlate salmon runs with climatic changes.

Among physical factors studied was the temperature regimen in pink salmon spawning areas. Temperature studies, at first carried on briefly in several streams in North Behm Canal, were later confined to Cabin Creek in Smeaton Bay, an arm of Behm Canal (Figure 1). This creek has a drainage area of 23.2 square kilometers, and is accessible to salmon for 1.7 kilometers to a point where a 6.4-meter falls blocks further ascent. The average annual pink salmon escapement during the period 1938 to 1954 was 18,000 and the maximum was 75,000 in 1941 (Martin 1959).

Specific objectives of temperature studies in Cabin Creek were (1) to determine interrelationships among temperatures of the air, stream, intragravel water, and groundwater in streambanks, (2) to evaluate effects of low air tempera-

¹ Contribution No. 76, College of Fisheries, University of Washington.

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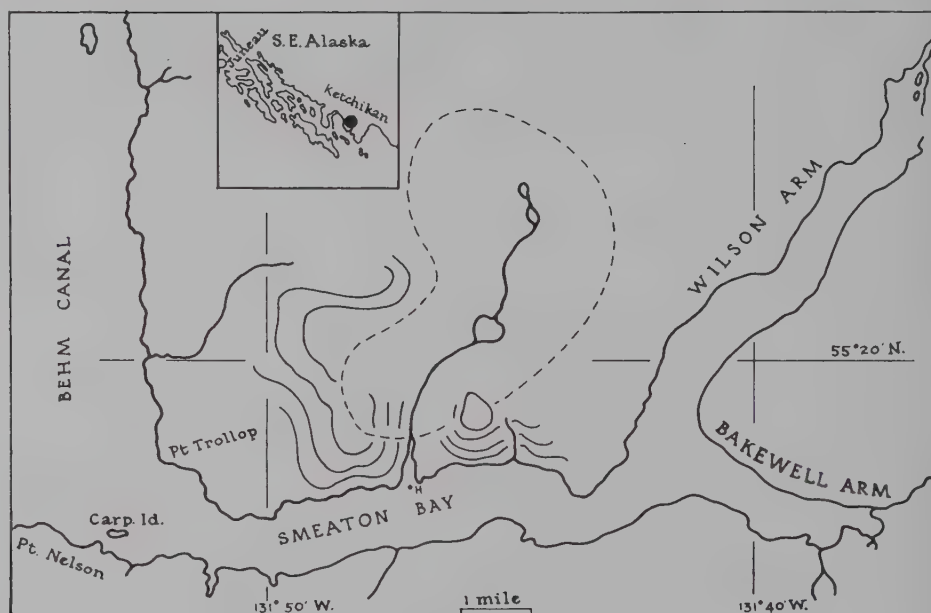


FIG. 1. Location of Cabin Creek showing drainage area.

tures on freezing of the streambed and survival of eggs and larvae, and (3) to measure streambed temperature gradations. This paper presents results of this investigation.

STUDY AREAS, EQUIPMENT AND METHODS

Two pink salmon spawning riffles in Cabin Creek, one at the 4.6 to 4.9 meter tide level, the other just upstream at the 5.2 to 5.5 meter tide

TABLE I. Location, depth and elevation above zero tide level of thermocouples in Area 1

Couple No.	Depth of couple under gravel in centimeters	Elevation of couple in meters above zero tide level
1	43.2	4.05
2	25.4	3.94
3	33.0	4.08
4	0.0	4.54
8	33.0	4.26
9	45.7	4.11
10	45.7	4.25
In stream	11	40.6
	13	38.1
	14	38.1
	16	45.7
		3.94
	5	71.1
	6	50.8
In bank	7	78.7
	12	43.2
	15	40.6

TABLE II. Location, depth and elevation above zero tide level of thermocouples in Area 2

Couple No.	Depth of couple under gravel in centimeters	Elevation of couple in meters above zero tide level
In stream	11	0.0
Vertical 1	12	12.7
	9	27.9
	10	50.8
		4.51
	15	12.7
Vertical 2	14	22.9
	16	40.6
	13	55.9
		4.48
In bank	7	12.7
	6	35.6
Vertical 3	5	48.3
	8	63.5
		7.99
	2	30.5
Vertical 4	3	53.3
	1	71.1
	4	99.1
		8.78

level, were selected as study areas. In these areas, 16 thermocouples were buried at various locations; some in the streambed, others in the banks (Tables I and II, Figure 2). Measurements were taken for 14 months, at first every day, then every other day, and finally, every 3rd or 4th day.

Maximum and minimum air temperatures were recorded daily (in °F) with U. S. Weather

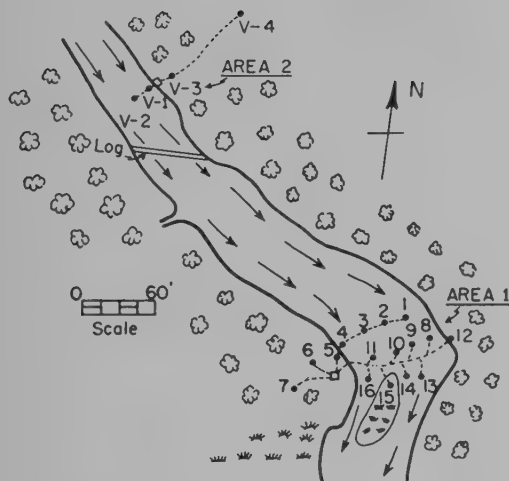


FIG. 2. Lower Cabin Creek showing location of thermocouples in Areas 1 and 2.

Bureau thermometers, and a daily average was computed in accordance with weather Bureau procedure. Stream temperatures were measured daily (in °F) with a calibrated Moeller mercury glass thermometer. Temperatures of intragravel water and groundwater were measured with copper-constantan thermocouples and a portable potentiometer. Measurements of intragravel water temperatures outside the study areas were obtained with either a Weston probe thermometer or a portable thermocouple mounted on the end of a thin rod. Temperatures of the bay were measured with a standard bathythermograph about one-half mile off the zero tide level of Cabin Creek.

Tests of readings between thermocouple No. 4 (in stream water) and a mercury thermometer were conducted. Readings were also tested between different observers and between successive readings by the same observer. No significant difference was found in any of the tests.

TEMPERATURE RELATIONSHIP

The degree of relationship between air and other temperatures varied with the season. During summer and fall months, stream temperatures were highest because of air temperature influence. This influence was not as strong during winter when the stream was covered with ice and snow, nor in the spring because of melting snow. For these reasons the discussion of temperature relationships is divided into three periods: (1) July to November, (2) December to February, and (3) March to June.

Period 1 (July to November)

Cabin Creek temperature data indicated a close relationship between temperatures of the different media during summer and autumn months. By far the closest relationship existed between temperatures of the stream and intragravel water ($r=0.99$); the least between air and groundwater temperatures ($r=0.63$) (Figures 3 and 4). The reason for the former probably lies in the direct interchange (Vaux and Sheridan 1960) between the 2 water layers and the latter is due

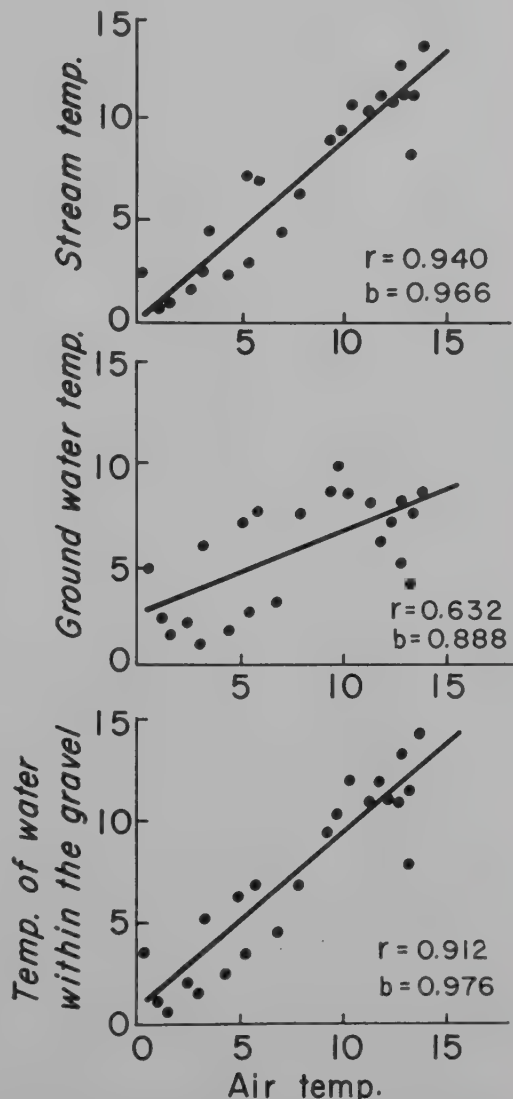


FIG. 3. Relation of stream, groundwater and water within the gravel temperatures to air temperatures (temperatures are two-week averages in °C).

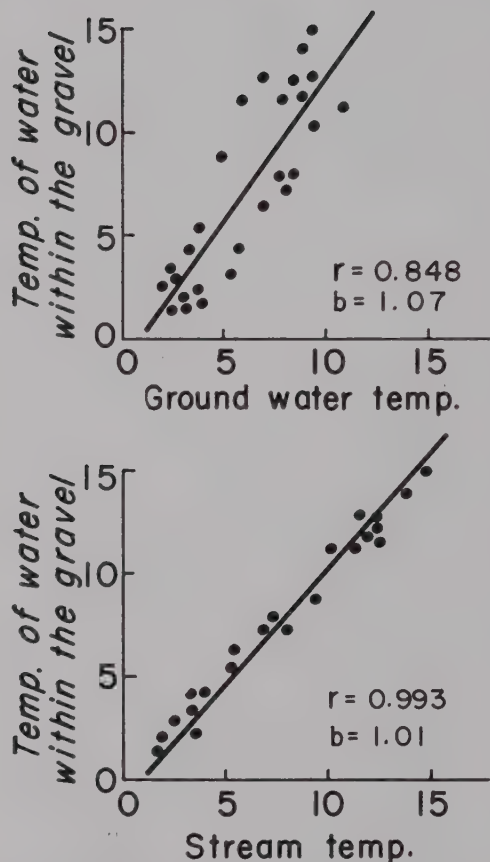


FIG. 4. Relation of temperatures of water within the gravel of the streambed to groundwater and stream temperatures (temperatures are two-week averages in $^{\circ}\text{C}$).

to a lag of groundwater temperatures. A similar lag in soil temperatures behind air temperatures was found by Bliss (1944).

During this summer and fall period, air temperatures exerted dominant influence over stream and groundwater temperatures. These in turn influenced temperatures of intragravel water of the streambed because of direct interchange on the one hand and groundwater seepage on the other. Such air temperature influence has been mentioned by Davidson *et al.* (1943), Pritchard (1944), and James (1956).

Period 2 (December to February)

The amount of change in temperature relationships of the various media with the onset of winter depends on whether the winter is "open" or "closed." During an "open" winter, air tem-

peratures are higher and little or no ice covers the streams, hence stream temperatures are under direct influence of the air. A "closed" winter is characterized by an ice and snow cover which interferes with air temperature influence. Ice and snow are good insulating materials for the streambed and protect it from freezing. Parsons (1949) writes, "as ice is a poor conductor of heat, the temperature gradient is steep and the rate of freezing from the bottom surface of the ice rapidly decreases as an inverse exponential function." Hazzard (1941) and Bay *et al.* (1952) have also reported on the protection afforded by ice and snow layers.

We were fortunate in being able to study the effect of low air temperatures during the coldest winter recorded in southeast Alaska for a number of years. During the winter of 1949-50, exceptionally low air temperatures occurred by the end of December and continued through January (mean air temperature for January was -10°C). Air and water temperatures, however, declined together until the stream was frozen. After that, air temperatures continued downward (as far as -15°C average daily temperature), but intra-gravel water temperatures leveled off slightly above 0°C , with the addition of an ice and snow layer.

With one exception, streambed gravel did not freeze in the study areas. The exception occurred in a 1,350 square foot area in Study Area 1, which froze to a depth of at least 30.5 cm. All salmon larvae in this area were dead and no aquatic insect larvae could be found, although they were abundant in adjacent areas.

Streambed freezing was apparently rather limited in the rest of the stream, for larva sampling conducted after the spring thaw in riffles as far upstream as the falls revealed only one other instance of numerous dead larvae. This, and the much above average return of 25,000 pink salmon of this year class indicates no unusual freshwater mortality.

Period 3 (March to June)

In the spring the effect of air temperature on stream temperature was modified by melting snow, which had accumulated during the winter along stream banks, hillsides and in the headwaters. In the spring, the warmer the air, the faster snow melts and runs into the stream. As snow-melt water usually enters at temperatures from 0° to 2°C , it reduces the influence of air temperature on stream temperatures. It is not until sometime in July that this interference disappears when most of the snow has melted. For example, high air

temperatures in June, 1950 had a minor effect on stream temperatures in Cabin Creek compared with the influence later in the season. Influence of air temperature in the spring depends then on the amount of accumulated snow, and on air temperatures, both of which vary from year to year.

Annual variation may be assessed in Cabin Creek by comparing the number of temperature units³ (t.u.) available for the same period in different years. For the period March 15 to June 15 there were 612 t.u. available in 1950, 524 in 1951, 875 in 1952, and 594 in 1953. This is a range of 351 t.u. or almost 20% of the total units required (1800) by the pink salmon for development to the state of emergence.

TEMPERATURE GRADATION IN THE STREAMBED AND STREAMBANK

Temperature gradation studies included upstream and intertidal areas in Cabin Creek. Upstream areas are above tidal influence. Here the extent of temperature gradation of intragravel water and groundwater in the bank depends on the season of the year. Gradation was not great in the streambed at any time of the year, but was more marked in groundwater, especially during the summer (Figure 5). The lack of marked gradation in the streambed emphasizes the close temperature relation between surface stream and intragravel water.

The intertidal zone is that part of a stream covered by saltwater on flood tides and uncovered

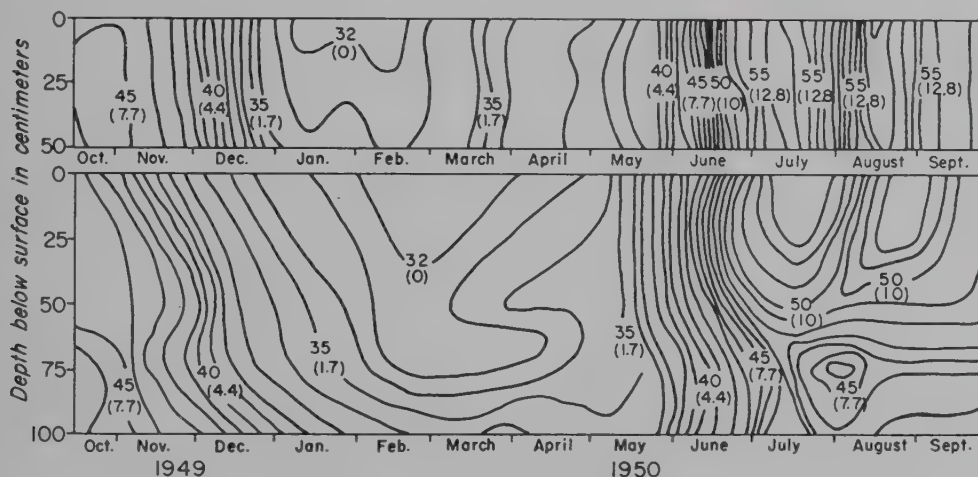


FIG. 5. Isotherms showing vertical gradation of water within the gravel of the streambed (upper) and groundwater in the banks (lower). (Temperatures in °F with corresponding temperatures in °C in parenthesis.)

on ebb tides. Water temperatures within the gravel in this zone are more complex than in upstream areas because here they are also influenced by saltwater temperatures, which are considerably different from freshwater stream temperatures.

In 1949-50, saltwater was much warmer than stream water during the winter months of December, January and February (Table III). Because of temperature differences it appears that if a water interchange or heat transfer occurs when the warmer saltwater bathes the colder intertidal zone during the winter, temperatures of water within the gravel would rise. The duration of temperature increases in the gravel would then depend on the time tidal waters remained over

different tide levels and on the length of time required for interchange to take place.

Evidence of this phenomenon was obtained in Cabin Creek by means of a portable thermocouple and later, a recording thermograph.

On February 10, 1950, measurements of intragravel water temperatures were started above tidal limits and continued down through the intertidal zone as the tide receded. One hour after low tide, measurements were repeated in an upstream direction. Saltwater temperature was 3.89° C and surface stream temperature was 0° C. Results of temperature measurements showed that at a depth of 30.5 cm in the gravel, temperatures were 2.78° C higher at the lowest station than at the upstream station (Figure 6). Stream water temperatures in the upper half of the intertidal zone were similar to upstream water temperatures

³ Temperature units are the number of degrees F above 32° F per day. These are accumulated daily.

TABLE III. Mean monthly temperatures in the stream and off the mouth of Cabin Creek. 1949-50. (Temperatures in ° C)

	Month	Streamwater	Saltwater
1949	August	11.67	12.78
	September	11.67	13.33
	October	7.72	7.78
	November	6.67	7.72
	December	2.22	4.44
1950	January	0.00	5.00
	February	0.56	3.89
	March	1.67	3.89
	April	2.22	5.56
	May	3.89	4.44
	June	10.00	5.56
	July	12.78	14.44
	August	13.33	14.44
	September	11.67	12.78

but in the lower half of the intertidal zone they increased gradually to the temperature of the sea. Water within the gravel in the entire intertidal zone did not become as cold as water within the gravel above tidal influence during the entire tidal cycle. In addition, at a depth of 17.8 cm in the gravel, cooling of 0.6° to 1.1° C occurred in the lower intertidal zone during a period of 1 to 5 hours.

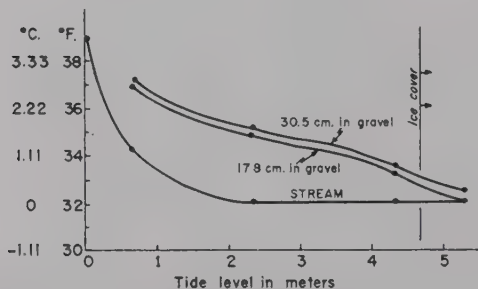


FIG. 6. Temperature gradient in the intertidal zone of Cabin Creek. February 1950.

Observations made at a later date with recording thermometers in the upper intertidal zones of Cabin Creek and the Wilson River (12 miles from Cabin Creek) furnished additional evidence that water temperatures within the gravel were almost immediately influenced by encroaching saltwater.

DISCUSSION

July to November Temperature Relationship

The dominant role played by air temperatures during the summer and fall months is important to the pink salmon, for any deviation in air temperatures from the normal would be almost immediately reflected in the salmon's environment.

Stream water temperature affects adult salmon during the spawning season and water temperatures within the gravel influence the development and survival of eggs and larvae.

Adult mortalities caused by high stream temperature are mentioned by Huntsman (1946), who reported death of *Salmo* and *Salvelinus* in New Brunswick and Nova Scotia because of high temperature and low stream flow. Royal (1953) reported that abnormally high water temperatures caused extensive mortality in unspawned adult sockeye salmon in the Fraser system. Institute colleagues observed large numbers of dead unspawned pink salmon in Snake Creek in 1949 and in Anan Creek in 1951. Tests in Anan Creek showed that death was due to a combination of large numbers of salmon, high stream temperatures, and low streamflow with consequent low levels of dissolved oxygen. Conditions in Snake Creek were similar.

Abnormal stream temperatures may also harm the young. Accelerated development due to high temperatures may result in out-of-step organ differentiation (Hayes 1949) or cause fry to migrate at the wrong time to meet the most favorable conditions (Martin 1958). High temperatures may be lethal to salmon eggs as reported by Donaldson (1954) and by Seymour (1956).

On the other hand, abnormally low fall air temperatures were shown by Hanavan and Skud (1954) to be associated with low freshwater survival of pink salmon in Sashin Creek, Little Port Walter, Alaska. Incubation at low temperatures has also caused mortalities in sockeye salmon eggs (Royal 1953).

In Cabin Creek, water temperatures during the months of October and November varied little from 1949 to 1954 (665 to 710 temperature units). A marked deviation occurred in 1955 (460 temperature units); however, we were not able to evaluate the effect of lower temperatures in the fall of 1955.

December to February Temperature Relationships

Ice and snow cover in Cabin Creek furnished a protective insulation against freezing of streambed gravels and no large scale mortality of salmon eggs was discovered in the stream. Therefore, the manner of formation of ice and snow cover may be a critical factor in survival. Davidson and Hutchinson (1943) stated that at Little Port Walter damage to eggs and larvae occurred when cold spells were accompanied by fair weather and little snow cover. When cold weather was accompanied by a heavy snowfall, the snow furnished protective insulation. Neave (1953) re-

ported freezing of eggs or larvae by coincidence of prolonged cold weather with exposure of spawn-ing beds to the air.

March to June Temperature Relationships

Evidence of the influence of spring temperatures on emergence and migration of pink salmon fry is presented by Hanavan and Skud (1954), who found a correlation of -0.881 between the time of seaward migration of fry and March-April stream temperatures. Variation in time of the spring fry migration may be important to survival as Martin (1958) reported a direct correlation between survival of fry and saltwater temperatures at the time of migration.

Studies have shown that in southeast Alaska the bulk of pink salmon fry have migrated by the middle of June and temperature records indicate that stream temperatures seldom exceed 10°C during this migration. Therefore, high temperatures are not likely to be a direct cause of mortality in freshwater at this time.

Temperature Gradation in the Streambed

While temperature gradation was not great in the streambed above tidal influence at any time of the year, warm saltwater contributed to higher intragravel water temperatures of the intertidal zones of the streams studied. This adds to the complexity of the temperature regimen in intertidal areas because intertidal zone temperatures are a result of (1) upstream water temperatures, (2) saltwater temperatures off the stream mouth, (3) time of exposure to saltwater, and possibly (4) the permeability of gravels, which governs the interchange between surface stream and gravel layers.

Intertidal zone studies conducted by the Institute in several southeast Alaska streams in 1949 showed that salinities of water within the gravel varied with the tide level and with elapsed time after the tide had ebbed. More extensive measurements made in one stream in 1948 also showed that the increase and decrease of salinities of water within the gravel of the intertidal zone depended on tidal ebb and flow. Skud (1954) reported that stratification revealed by salinity sampling in Lover's Cove Creek, southeast Alaska, indicated that the gravel bottom did not impede the exchange of freshwater and saltwater. He stated that in general freshwater within the streambed during an ebb flow varied little from the recovery in the layer of water just above the streambed.

Changing temperatures and salinities create, in the intertidal zone, an environment distinct from

the rest of the stream. We have observed large numbers of pink salmon spawning in intertidal zones of many streams in southeast Alaska, on Kodiak Island and in Prince William Sound. The importance of intertidal zone spawning was recognized by Dr. William F. Thompson as far back as 1948 and led to research on the effects of seawater on salmon embryos (Rockwell 1956). Hence it is of interest to comment on the possible effects of the different temperatures and salinity patterns in intertidal zones.

Saltwater temperatures exceeded freshwater temperatures in Cabin Creek during the winter months when low temperatures can be a critical survival factor. Higher saltwater temperatures warmed the water within the gravel to a depth of at least 30.5 cm for varying lengths of time. Therefore, it may be postulated that adverse effects of extremely low air temperatures during periods of low snowfall would be tempered by warm saltwater. In such cases survival could be much higher in the intertidal than in upstream areas. This point was brought up by Hanavan and Skud (1954) who wrote that abnormally low stream temperatures resulting in a low freshwater survival rate may be modified by warmer tide-water to create conditions most favorable for survival at some intermediate tide level.

Another effect of warmer saltwater over the intertidal zone would be an increase in the development rate of pink salmon eggs and larvae, since more temperature units are available for growth. Although no published works have shown that different developmental rates exist between intertidal zones and upstream areas, it is known that in Cabin Creek and numerous other streams, intertidal zone areas are used last by the spawning pink salmon.

The effect of mild saline water on salmon eggs and larvae is also apparently beneficial, for eggs reared in dilute saltwater have a higher survival than eggs in freshwater controls (Rockwell 1956).

CONCLUSIONS AND SUMMARY

The temperature regimen in 2 pink salmon spawning riffles in Cabin Creek, southeast Alaska, were studied for a period of 14 months in 1949-50. These studies were undertaken because little was known of the temperature regimens of streams in the area and because survival of both adult and young pink salmon in freshwater depends in part upon suitable water temperatures.

Temperatures of the air, stream water, intra-gravel water, and bank groundwater were measured. A multiple thermocouple system was in-

stalled in each of 2 spawning riffles to measure temperatures in the gravel and in the banks.

Analyses of temperature data showed the following:

1. Although the extent of relationship between temperatures of the various media varied with the season, air temperatures were found to dominate and govern all water temperatures during a large part of the climatic year.

During the summer and fall months, the closest relationship existed between temperatures of stream water and intragravel water ($r = 0.99$); the least between air and groundwater temperatures ($r = 0.63$). Because of close agreement between air and stream and intragravel water temperatures, abnormal air temperatures can affect pink salmon adult spawners as well as eggs and larvae.

2. Winter stream temperatures depend to a large extent on whether the stream is covered with ice and snow. If the stream is clear of ice, stream temperatures are usually higher than when the stream is covered. If the stream is covered, temperatures in the stream are less influenced by air temperatures. The protective influence of an ice and snow layer was evident in Cabin Creek during one of the coldest winters on record.

3. In the spring, melting snow subdues the effect of high air temperatures on water temperatures. Variable yearly water temperatures in the spring, caused by an interaction of air temperatures and accumulated snow, can influence the number of temperature units available to developing pink salmon larvae, hence may cause fry to migrate to sea at unfavorable times.

4. Temperature gradation was more pronounced in groundwater of the banks than in water within the gravel of the streambed, and was more marked in the intertidal zone than in the stream above tidal influence. In the intertidal zone, temperature gradation was the result of ebb and flow of warmer saltwater over the area. Temperature changes in the intertidal zone depend mainly on tide level, temperatures of stream and saltwater, and permeability of streambed gravels.

Saltwater bathing intertidal zones may give salmon eggs and larva protection against freezing during extremely cold winters and may accelerate developmental rate because of higher temperatures than in the stream above the tides. Pink salmon eggs reared in dilute saltwater also have a higher survival than eggs reared in freshwater controls.

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CALLING AND SPAWNING SEASONS IN A MIXED POPULATION OF ANURANS¹

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INTRODUCTION

This work was done to learn the relation between the period in which male anurans vocalize and the actual times of spawning and to learn the reproductive seasons of a sympatric group of anuran species. Precise knowledge of the reproductive season, including environmentally induced variations, in a group of species that utilize the same breeding pools is important in assessing the possibilities of interspecific hybridization and in respect to possible interspecific competition, particularly in the larval stage.

This report concerns primarily the 7 species of anuran amphibians that breed regularly in a farm pond ("tank") and in a few subsidiary catchments of temporary waters. These include one toad (*Bufo valliceps*), 3 hylids (*Pseudacris streckeri*, *P. clarki*, and *Acris crepitans*), one microhylid (*Microhyla olivacea*) and 2 ranids (*Rana pipiens* and *R. catesbeiana*). The data represent 4 years of observation to February, 1960. Notes were made of the species of anurans calling on most nights of the 4 years. Records were also kept on evidence of reproductive activity (amplectant pairs, egg masses, and ovulated females) during examination of the breeding pools in various studies of anuran biology. Except for the 2 species mentioned below, absence of spawning records from the data does not necessarily mean that none occurred, for it was not practicable to search exhaustively for mated pairs of all species. Two of the 7 species were studied more intensively than the others. The Mexican toad (*B. valliceps*) has been censused through toe-clipping and recording of individuals in breeding aggregations since 1951 (Thornton 1960, Blair 1960). The leopard frog (*R. pipiens*) has been under similar observation through 1958 and 1959. The meteorological data are from the Austin Weather Station approximately 2 miles away.

METEOROLOGICAL CHARACTERISTICS OF THE FOUR YEARS

The reproduction of amphibians is influenced by both intrinsic rhythms (under hormonal control) and environmental factors (chiefly temperature and moisture). Our evidence is only indirect

and inferential in respect to intrinsic factors. In understanding the effects of environmental factors, and in attempting to relate these effects to possible internal periodicities, it is necessary to examine the major meteorological characteristics of the 4 years, which showed wide variation.

1956

The outstanding feature of 1956 was that it was the culminating year of several years of regional drought. The environment for amphibians in this year was influenced both by shortage of rainfall and by the cumulative effects of preceding years of deficient rainfall. This year may be characterized as abnormally dry, with a long, hot Summer season (Figure 1). The tank and other potential breeding pools dried completely in September of the preceding year. Calling and breeding activity were strongly correlated with the 3 rains of one inch or more in 24 hours that fell in 1956; total rainfall for the year was only 15.41 inches. The first of these rains (1.44 inches on February 8) resulted in limited accumulation of water and was followed by strong calling activity by 3 species (*P. streckeri*, *R. pipiens*, and *A. crepitans*), and the first 2 of these at least bred shortly after the rain. The remainder of February, all of March, and the first 22 days of April were virtually without rain, and the calling activity tapered off and ceased. Calling of *R. pipiens*, *A. crepitans* and *B. valliceps* started after 0.45 inches of rain on April 23, and these 3 species, plus *P. clarki* and *M. olivacea*, were activated by the 2nd heavy rain of the year (2.09 inches on May 1). At least 3 species (*B. valliceps*, *M. olivacea* and *R. pipiens*) bred soon after this rain, and it seems likely that 2 others (*P. clarki* and *A. crepitans*) did likewise, although no pairs were found. Calling tapered off as further rains of any consequence failed to materialize, and *A. crepitans* continued calling until the tank became completely dry on July 15. The 3rd heavy rain (1.95 inches on December 18) was followed by choruses of *P. streckeri*.

No records of the species calling were made on the following dates: February 25; April 1, 26-30; May 4-5, 25-26; June 14, 16, 19-25.

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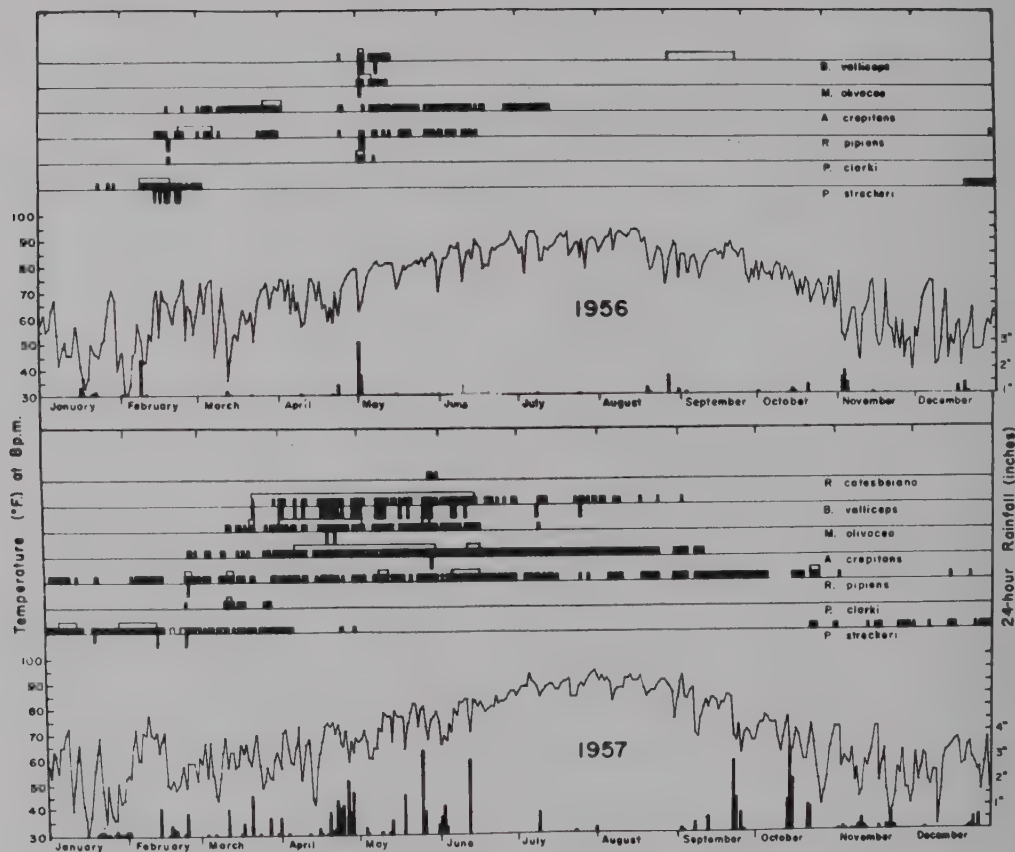


FIG. 1. Relations between evening temperatures (curves), rainfall (bar graphs), and reproductive activities of 7 species of anurans in 1956 and 1957. For each species, rectangles above line indicate periods of calling (unshaded refer to audible but distant calls). Brackets above delimit periods of peak calling. Rectangles below the line represent nights on which amplexant pairs were found.

1957

This was the wettest of the 4 years, with a rainfall of 51.30 inches and with 19 days that had rains of one inch or more. All of the local species of anurans, except *R. catesbeiana*, which was reinvading the area after being apparently extirpated by the drought, and *P. clarki*, showed a prolongation of their calling and breeding activities during the excessively wet Winter and Spring (Fig. 1). July had little rain, and August had none, but even so, calling by *B. valliceps*, *A. crepitans*, and *R. pipiens* occurred through this period, apparently in response to the ample water available in the breeding pools from the excess rainfall of winter and spring. A downpour of 6.78 inches in the period of October 13 to 15 was followed by calling of *P. streckeri* which continued into the 1958 reproductive season.

No records of the species calling were made on March 2, 15; May 4; December 26.

1958

This was a year of greater than average rainfall (41.02 inches), and it had 11 days with rains of one inch or more. One apparently significant feature was the relatively cold winter-spring period. The first day with an evening (8 p.m.) temperature of 70° or above did not come until March 7, by comparison with January 28 and 8, respectively, in 1956 and 1957, and the first period with two or more consecutive evening temperatures this high did not come until April 21, by comparison with March 4 and January 8, respectively, in 1956 and 1957. Two summer rains (2.47 inches on June 16-17 and 3.23 inches on July 5-6) were significant in stimulating *B.*

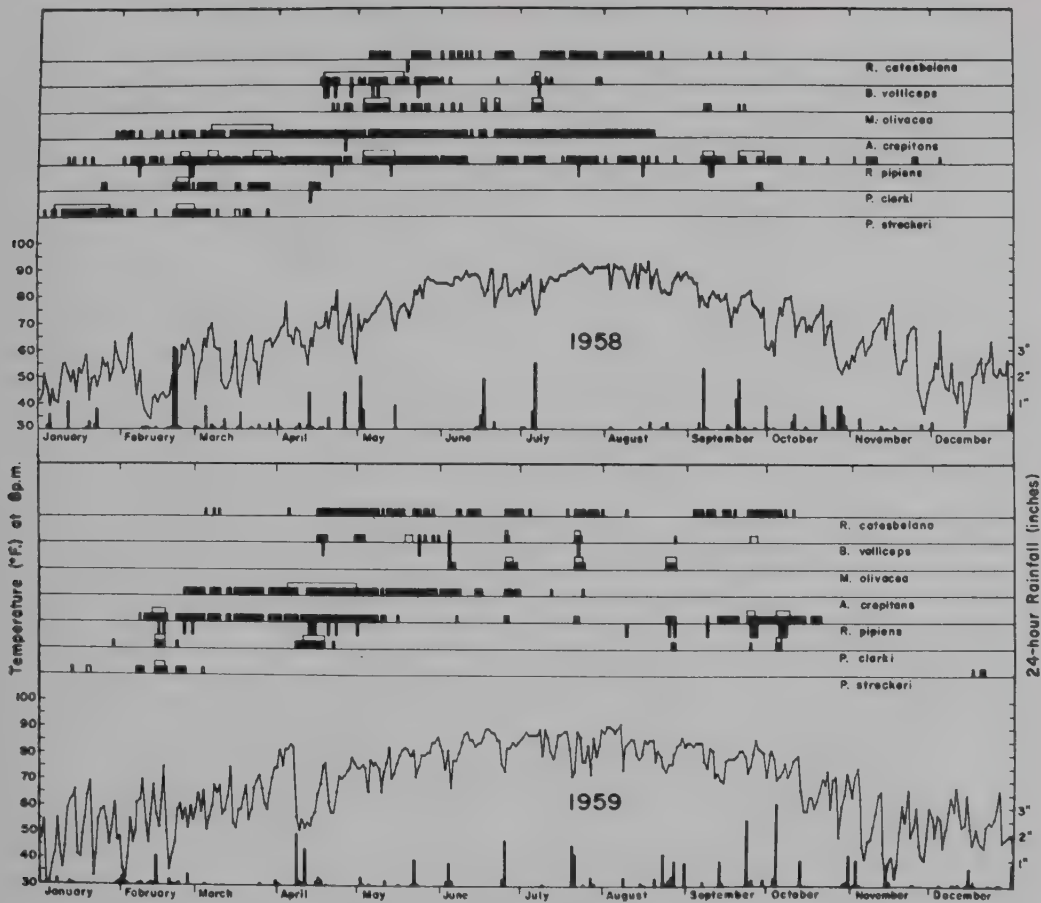


FIG. 2. Relations between evening temperatures (curves), rainfall (bar graphs), and reproductive activities of 7 species of anurans in 1958 and 1959. Explanation as for Fig. 1.

valliceps and *M. olivacea* and apparently in influencing the continued calling of several species through the Summer (Figure 2). Two September rains (2.26 inches on September 7 and 3.09 inches on September 19-20) stimulated activity by *M. olivacea* and *R. pipiens*. There were no further heavy rains in this year, and the 1959 calling season of *P. streckeri* did not start until after the start of that year.

No records of the species calling were made on April 1; May 2; September 24-26.

1959

This was a year of nearly average rainfall, with 34.96 inches, but the distribution of the 15 days with rain of one inch or more was unusually even after a relatively dry winter-spring season (Fig. 2). January and February were without heavy rains, but every other month except December

had one or more. A rain of 1.06 inches on February 14 was followed by activity of *P. streckeri*, *P. clarki*, *R. pipiens*, and *A. crepitans*. A rainy period of 3.51 inches from April 8 to 11 was followed by calling of *R. catesbeiana* and *B. valliceps*, with spawning by the latter, and by a second period of activity of *P. clarki*. It was also followed by a 2nd period of spawning by *R. pipiens* and by continued activity of *A. crepitans*. Calling by *M. olivacea* was first heard after a rain of 0.88 inch on June 4, and this species was activated by a heavy rain later in June, one in late July and one in late August. These summer rains also stimulated activity by all of the other species except the 2 *Pseudacris*, of which *P. clarki* called only after the August rain. Late summer and early fall rains through October 4 stimulated calling and spawning by *R. pipiens* and calling by *R. catesbeiana* and *P. clarki*. Call-

ing by *P. streckeri* started after a rainfall of 0.93 inch on December 15-16.

The winter-spring season was relatively cold, although not as much so as in 1958. The first evening temperature of 70° or above did not come until February 9, and the first period of 2 or more consecutive days of such temperatures was delayed until March 24.

No records of the species calling were made on March 27-28; June 9-10; August 23; October 15-16.

SPECIES ACCOUNTS

Observation of the local species of anurans through the 4 years that included extremes of moisture conditions provides a fairly adequate picture of the reproductive activities of these animals in relation to environment. The 7 species are treated individually below in respect to their responses to the progression of the seasons and to variations in weather.

Pseudacris streckeri

This is a winter-breeding species, as pointed out by Jameson (1950). The start of the calling season is quite variable and may come anywhere from October to January (Figs. 1, 2). The earliest call record was made on October 22, 1957, and the latest first call record was made on January 23, 1956. The initiation of the calling season in 4 of 5 years (including 1960) followed soon after rains of 0.70 inch or usually more. The initiation of the calling season in these winter breeders seems to be controlled largely by the occurrence of heavy rainfall and by a drop in temperature below those temperatures characteristic of late summer and early fall.

The October start in 1957 was much earlier than in other years, but it is apparently explained by a combination of excessively heavy rainfall (6.78 inches on October 13-15 and 2.01 inches on October 21-22) and a sharp downward break in temperatures after passage of the respective frontal systems, with a minimum of 32° F being recorded after the 2nd one. Calling started after mid-December rains in 2 years (1956, 1959) and it was delayed until approximately mid-January in 2 years (start of 1956 and 1959 seasons). The delay of the start until January in these 2 years seems attributable to inadequate moisture in the fall. In 1955, the 2.41 inches of rain in November and December was ineffective in providing ground moisture because of the effects of the preceding months and years of drought. Similarly, November and December of 1958 were relatively dry, with only 1.15 inches of rainfall through December 28 and with this coming in 7 scattered days

with rains of less than one-half inch. A rainfall of 1.07 inches on December 29-30, 1958, was probably influential in the start of the 1959 calling season. This rain was followed by a period of inhibitory low temperatures, and calling started on January 13, on the 2nd day of light rain with evening temperatures above 60°.

The development of the calling season shows a rather consistent pattern. Even though ordinarily initiated by heavy rains, the calling season develops slowly, and for the first several nights there may be no more than one to 3 individuals calling. In 1956, when potential breeding pools were dry, scattered individuals called in nearby fields on January 23, 27 and 29 before moving to the tank which had caught rainwater on February 8. The first individuals heard ordinarily call in late afternoon; if temperatures drop sharply after sunset, there is no evening calling during this phase. Calling is sporadic, and periods of calling (mostly brief) usually require an external stimulus such as the noise of passing airplanes. Once the calling season starts, large choruses and peak calling effort usually follow heavy rains. At such times, the choruses usually continue day and night, virtually without interruption, for several days so long as meteorological conditions remain favorable. During these peaks, calling will usually continue as the temperature drops at night to levels that would be inhibitory at the start of the calling season. Examples from calling peaks in 1956 and 1957 are illustrative of this behavior. On the cloudy nights of February 8 and 9, 1956, the frogs called through the night and were still calling at 7:00 a.m. as the temperature dropped from 43° at 8 p.m. to respectively 42° and 40° at 7 a.m. On the cloudy night of January 25, 1957, the frogs were calling in the evening with an 8 p.m. temperature of 38° and they were still calling at 7 o'clock the next morning with a temperature of 33°.

Since they breed at the season in which the lowest temperatures of the year occur, the activities of these frogs are strongly influenced by the march and countermarch of cold Arctic and warm Gulf Tropical air masses (Figs. 1, 2). Calling has been observed on days with evening temperatures ranging from 35 to 78° F, with a median of 56.5° (Figure 3). Once the males reach the pools, they apparently remain there through the calling season, as calling is quickly resumed with warming after passage of a cold front.

Breeding, as indicated by amplexant pairs, was observed in 1956 and 1957, following heavy rains and during peak periods of calling (Fig. 1). Evening temperatures at which amplexant pairs

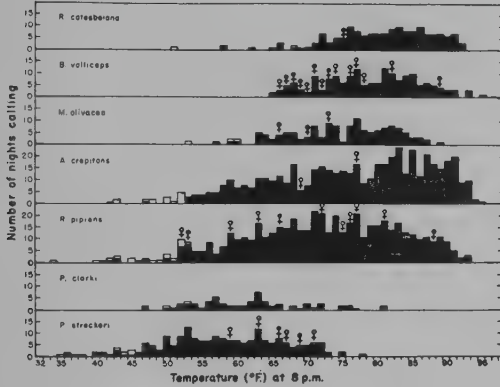


FIG. 3. Frequency distributions of evening (8 p.m.) temperatures on days when calls were heard. Unshaded symbols refer to daytime calling. Female symbols refer to evening temperatures at which amplexus was observed.

were found ranged from 59 to 71°, with a median of 65°. Breeding came at almost the same time in the 2 years (February 14 to 23 in 1956 and February 13 to 24 in 1957), but there is evidence that breeding may come at other times in the calling season. Jameson (1950) reported breeding on January 23, 1949. A recently metamorphosed individual, found on January 10, 1960, indicates that at least one individual laid eggs in the mid-December period of activity of 1959. This shows that breeding can occur at the very start of the calling season or at other times in it, although the peak of reproductive activity appears to come in late February. No record of breeding activity was obtained in 1958 or 1959 for reasons to be discussed below.

After the peak calling periods, the choruses decreased rapidly, and only one or 2 individuals could be heard per night as the calling season came to an end. The end of calling in the first week of March in 1956 and 1959 is possibly attributable to the scarcity of rainfall in that month of those years. March was relatively wet in 1958, and calling did not end until March 28 in that year. The prolongation of calling by a few individuals until April 29, 1957, is possibly attributable to the excessive rainfall in March and April.

One interesting aspect of the activities of this species was a change of breeding pools in apparent relation to weather-related changes in the pools. Prior to the regional drought, *P. streckeri* was rarely found in the tank, which had the aspect of permanent water and which was heavily populated by largemouth bass (*Micropterus salmoides*) and bluegills (*Lepomis macrochirus*). In 1956 and 1957, drying up of the tank in each preceding year resulted in it having the aspect of

a temporary, runoff pool without permanent vegetation and without fish, and these frogs bred there in large numbers. Largemouth bass and mosquito fish (*Gambusia*) were stocked in the tank in the spring of 1957, and duckweeds (*Lemna* and *Wolffia*) appeared there. In 1958 and 1959, the tank had the aspect of permanent water and was virtually covered by a mat of duckweed and filamentous algae. The tank was ignored by *P. streckeri* in these 2 years, and this species congregated in an old gravel pit about 500 feet away and in pools in an intermittent stream and its tributaries. The dispersion of the population in 1958 and 1959 was largely responsible for the lack of mating records in those years. Additional work is needed to determine the cues used in the apparent rejection of the "permanent" water by these frogs.

Pseudacris clarkii

This species quickly forms large choruses after heavy rains in late winter and early spring and in late summer and early fall, but there was no evidence that it does so in mid-summer. It is best characterized as an opportunistic breeder, but one with a limitation to spring and fall seasons. The general pattern of the calling, and apparently of the breeding, season is very different from that of *P. streckeri*. There is no gradual build up of choruses such as occurs in that species, and the males usually continue to call for a shorter time after the peak has been reached. Winter rains may cause a few individuals to call briefly, then later rains will trigger off peak choruses. This is best illustrated by considering the spring season in each year. In 1956, one individual was heard on February 19 and 11 days after a heavy rain, but the species was not heard again until a rain in excess of 2 inches on May 1 was followed by 3 days of heavy chorusing. One individual called 4 nights later, and the species was heard no more in that dry year. In 1957, one individual called on February 24 after 0.89 inch of rain on the previous day, and one called on March 11, which had 1.04 inches of rain. There were large choruses on the 2 following days, and after that there were only scattered individuals calling until the last one of the year was heard on March 28. In 1958, a few individuals called on January 25 and 26 as the temperature increased after 0.95 inches of rain on January 22-23. No more were heard until strong choruses developed after 6.05 inches of rain on February 21-22 and lasted through February 26. Scattered individuals were heard, except as inhibited by temperature drops, through March 28. The spring calling season

ended with 4 days of calling by few individuals after 1.38 inches of rain on April 13. In 1959, one was heard on January 29, which was the 4th cloudy day with traces of rain, but no more were heard until February 14, when a rain of 1.06 inches set off a 4-day period of strong chorusing. Calls were heard again on February 22, after a 4-day interruption by cold, but they were not heard again until strong choruses were stimulated by 1.97 inches of rain on April 8. These lasted through April 18, and a few individuals gave the last calls of the spring season on April 22.

Late summer or fall choruses were formed in 1958 and 1959. In 1958, a few individuals were heard on the nights of September 27 and 28. There had been 3.09 inches of rain on September 19-20, and this activity probably resulted from that rain. I was away on September 24-26, and no record is available for those days. In 1959, choruses were formed following heavy rains on August 27, September 23, and October 4, but none lasted more than 2 days. The strongest chorus was formed on October 4 and 5, after a rain of 3.22 inches on the former day.

This species is like *P. streckeri* in that calling continues day and night during the peaks of calling activity after heavy rains. The evening temperatures on days these frogs call are somewhat higher than for that species. The range is from 47 to 81° F, and the median is 63°. No records of breeding were obtained, principally because these frogs called mostly from subsidiary pools that were not systematically checked for amplexant pairs. Numerous amplexant pairs were found on April 13, 1958, about 10 miles southeast and following a heavy regional rain (Fig. 2). Lindsay (1958) reported clasping pairs as early as February 4, 1952, and as late as October 3, 1953, and on various other dates in February, March, and April in the Austin area. I suspect that females of this species may lay more than one set of eggs per year, from the evidence of their spring and fall breeding seasons, but close observation of marked populations will be necessary to show whether or not this is so.

Rana pipiens

The leopard frog is a winter-spring and early fall breeder in this area. It is the 2nd species (after *P. streckeri*) to start calling in winter. The start of the calling season varied from December 15 of the preceding year to February 14. The date and situation on the first day of calling were as follows in the 4 years: 1956, February 14, 5 days after heavy rain, with evening temperature of 71°; 1957, December 30, 1956, 11 days after heavy rain, with evening temperature of 62°;

1958, December 15, 1957, without recent rain and with evening temperature of 63°; 1959, February 8, with light rain and evening temperature of 62°. The build up in the calling season is very much like in *P. streckeri*. Only a few individuals are heard at the beginning of the season; these first call in the afternoon, and if temperatures remain high enough they will continue calling after dark. Strong chorusing and mating are stimulated by rainfall (Figs. 1, 2). At such times each individual calls persistently, there are many more individuals calling, and a vocal variant that may be described as a "chuckle" is added to the usually heard, pulsed call. Temperature extremes, both low and high, influence the calling. Most calls are heard on nights when the evening temperature is above 51° F (Fig. 3), but the range is from 41 to 93°, with a median of 67°. The lowest temperature at which any calling was heard was on February 12, 1958. There was light snow on the night of February 11, and the temperature dropped to 28° at 7:00 o'clock the next morning. With bright sun, calls were heard at noon with an unofficial temperature of 35°, while the official Weather Bureau temperature at that hour was 30°.

Calling continued intermittently through the summer in all but 1956, in which year the end of the calling preceded complete drying up of the tank on July 15 by 2 days. In the relatively wet years of 1957 and 1958, some calls could be heard on most nights of summer, while in the dryer year of 1959 summer calling was correlated with heavy rains. Peak choruses again developed after heavy rains in late summer and early fall of all years except 1956. On hot days of mid-summer calling tended to be done mostly after midnight.

The evidence is fairly good as to the spawning periods of the species both because it is relatively easy to obtain and because of the intensive study by marking and recapture in 1958 and 1959. There is a rather sharp demarcation of the winter-spring and fall breeding seasons (Table I) even though males continue to call through the summer. With the records for the 4 years summarized, the winter-spring season extends from February 8 to May 13, with an apparent gap from about mid-March to about mid-April. This gap may reflect the scarcity of March and early April rainfall in the 3 years (1956, 1958, and 1959) in which most of the breeding evidence was obtained. The fall season extends from July 22 to October 14, and, as in the winter-spring season, the peaks of activity usually follow heavy rainfall. As may be seen from Table I, the 2 breeding seasons appear to be approximately

equal in terms of their probable significance in maintenance and replacement of the breeding population. Observations of marked individuals (to be published in detail in a later paper) show that the same individuals, both male and female, participate in both breeding seasons if they survive.

TABLE I. Seasonal distribution of reproductive activities of *Rana pipiens* and *Bufo valliceps*. Summary of available information, 1955-1959

Periods	RANA PAPIENS						BUFO VALLICEPS
	Egg masses	Pairs in amplexus	♀ with oviductal eggs	Gravid ♀♀	Spent ♀♀	Totals	Pairs in amplexus
Feb. 1-14.....	—	1	—	1	—	2	—
Feb. 15-28.....	6	3	2	8	2	21	—
March 1-14.....	—	—	—	—	5	5	—
March 15-28.....	—	—	—	—	—	—	1
March 29-Apr. 11.....	—	—	—	—	—	—	31
April 12-25.....	6	3	—	—	—	9	37
April 26-May 9.....	1	2	—	2	—	5	36
May 10-23.....	—	—	1	—	—	1	2
May 24-June 6.....	—	—	—	—	—	—	20
June 7-20.....	—	—	—	—	—	—	—
June 21-July 4.....	—	—	—	—	—	—	—
July 5-18.....	—	—	—	—	—	—	6
July 19-Aug. 1.....	2	—	—	—	—	2	2
Aug. 2-15.....	1	1	—	—	—	2	—
Aug. 16-29.....	2	—	—	—	1	3	2
Aug. 30-Sept. 12.....	1	2	2	12	—	17	—
Sept. 13-26.....	—	3	6	4	—	13	—
Sept. 27-Oct. 10.....	4	4	4	5	—	17	—
Oct. 11-24.....	—	—	—	—	1	1	—
Totals.....	23	19	15	32	9	98	137

The range of temperatures at which spawning has been observed (Table I) is greater than for any other of the species. The range is from 52 to 88° F, with a median of 70° (Fig. 3). There is little overlap, however, between temperatures in the winter-spring and fall breeding seasons. The range in the former is from 52 to 77°, with a median of 64.5, while in the latter season it is 72 to 91°, with a median of 81.5°.

The wide range of temperature tolerance (5-32° C = 41-90° F) for *R. pipiens* embryos from Louisiana reported by Moore (1949a) probably relates to this split breeding season. Water temperatures are not directly related to air temperatures, and the differences in the former were undoubtedly less at the 2 seasons than were those in air temperature. Nevertheless, a wide range of water temperatures is indicated.

The relation of the individuals of this species to the breeding pool is somewhat different from that of any other of the local species. Some individuals may be found living around the margin of the tank at any season of the year. Others apparently come to the pool only for a period of days

in which spawning occurs. One female in the fall breeding season of 1959 is known to have moved to the tank from where she lived about 100 feet away and to have returned there after spawning. At least some of the females appear at the pool several days before they are ready to lay. The females may pass the eggs into the oviduct as much as 24 hours before they are found in amplexus.

Rana catesbeiana

The local population of bullfrogs declined through the years in which the tank dried up, and it apparently became extirpated before the beginning of the 1956 season. No bullfrogs were seen, nor were any calls heard, in 1956. One large female was released in the tank in the spring of 1957, and a few apparently immigrant animals appeared with the result that a few calls were heard in May. The population was well reestablished in 1958 and 1959, and the data for these 2 years are taken as representative of a stable population.

The calling season of this species corresponds more closely to the hot, summer season than does that of any other local species. The first calls of 1958 were heard on May 5, when evening temperature was 71° and following 2.72 inches of rain on May 2-3. The first calls of 1959 were heard in the afternoons of March 5 and 8, which had respective evening temperatures of 51 and 68°, and the first evening call was heard on March 10, with an evening temperature of 68°. Calls were heard rather consistently after April 16. The general pattern of calling in these highly aquatic frogs differs from that of the other species. Choruses were never heard, even after heavy rainfall. Instead, only one to 3 individuals might be heard at the same time even though many times that number of males were present in 1958 and 1959. This pattern continues through the summer, with the summer rains each being followed by several days in which a few individuals call (Fig. 2). Even in mid-summer, calls may be heard at any daylight hour as well as at night.

The last calls in 1958 were heard on September 22, and the last ones of 1959 were heard on October 11. Temperatures were showing a downward trend at that season. The first cool period of fall, with evening temperatures below 60° came within a few days after the last calls were heard in each year, and this may be significant in accounting for the nearly 3-week difference in the end of calling in the 2 years.

Evening calls were heard at temperatures ranging from 58 to 92°, with a median of 75°, but the distribution is skewed strongly in the direction of

the higher temperatures (Fig. 3). Amplexus was noted only on May 19, 1958, when the evening temperature was 75° and 4 days after a rainfall of 0.91 inch. Our information about reproductive season is consistent with Moore's (1942) evidence for temperature range in Louisiana embryos. He found that 14.8° C (= 59° F) was the lower limit for normal development, and 32° C (= 90° F) was the upper limit.

Acris crepitans

The cricketfrog is similar to the bullfrog in that it is a highly aquatic and littoral species, of which the population remains permanently resident in and around the pools in which breeding will occur. It is also much like the bullfrog in that calling usually continues through most of the hot, summer season. It differs in that it will call at considerably lower temperatures.

The calling season in all 4 years started with a few days of afternoon calls, followed eventually by evening calling as evening temperatures, in every year, remained higher than on any of the preceding days on which afternoon calling was heard (Figs. 1, 2). In 1956, day calling was first heard on February 18, and night calling was first heard on February 24, when the 8 p.m. temperature was 75°. In 1957, day calling started on February 25, and night calling was first heard on March 10, with an evening temperature of 69°. In 1958, day calling started on January 30, and night calling started on February 4, which had an evening temperature of 64°. In 1959, daytime calling started on February 25, and night calling started on March 8, with an evening temperature of 68°. Both the start of the calling season and the change to night calling appear to be determined by temperature rather than by rainfall. There is no clear relationship between rainfall and either of these, and the change to night calling came without any recent rain, but with increased evening temperatures.

The end of the vocal season varied considerably from year to year, but it always came before the end of the hot, summer season. In 1956, calling ended on July 13, two days before the last water evaporated from the tank. In the very wet year of 1957, calling continued until September 10, but heavy rains later that month and in mid-October failed to stimulate this species. Vocalization in 1958 ended on August 19 after several weeks of hot, dry weather, but heavy rain in early September did not result in any resumption of activity. Calling in 1959 ended on July 24, even though this was a relatively wet summer, and various heavy rains in August and September failed to induce further activity.

The peaks of calling activity came in March or April and showed little relationship to heavy rainfall (Figs. 1, 2). The peak periods were: March 25 to April 2 in 1956; April 7 to May 30 in 1957, with a 2nd peak from June 12 to 16 that apparently resulted from a heavy rain; March 6 to 29 in 1958; and April 5 to 30 in 1959. After the peaks were passed the calling in the remainder of the season usually involved few individuals and sporadic efforts. This is a day-night caller. At the peaks, the choruses may be continuous through all hours. After the peaks, the few individuals that do call may do so either in daytime or at night.

Vocalization occurs at a very wide range of temperatures. The lowest temperature at which daytime calling was heard was 41° at 5 p.m. on March 18, 1958, when a few individuals were stimulated to call by the sound of metal striking metal. The lowest temperature at which nighttime calling was heard was 44° at 10 p.m. on March 17, 1958, when a few individuals were heard calling weakly (8 p.m. temperature of 47°). Aside from this record, all night calls were heard at temperatures of 53° or above. The maximum evening temperature at which calls were heard was 95° (Fig. 3).

The few records of amplexant pairs (May 29, 1957, and April 26, 1958) were obtained at 69 and 77° and after heavy rainfall. Females with ripe eggs were noted on April 5, 1959, but no pairs were found. Pyburn (1956, 1958) followed this same population closely through toe-clipping and censusing in the years 1952 through 1955. He reported the first date of amplexus in 1953 as March 18 and the last date as May 10. He reported the last date of amplexus in 1954 as May 20. He also obtained evidence that a female may lay twice during this spring breeding season. In 1955, he observed a 2nd breeding season beginning in July and involving almost entirely animals from the relatively small generation produced in the spring breeding season of the same year. In this 2nd season, he found the first females with eggs on July 23 and the last on September 15.

Microhyla olivacea

The narrow-mouth frog is an opportunistic breeder that has its calling and spawning largely controlled by the occurrence of heavy rainfall. Some variations in behavior were noted, however, in the 4 years. The earliest date of calling was March 12 (of 1957), and the latest date of calling was September 22 (in 1958). Within this span, reproductive activities are strongly influenced by rainfall.

In dry 1956, the one period of activity came after the one heavy rain in early May (Fig. 1). A few individuals called on the night of May 1, after 2.09 inches of rain in the afternoon and with an evening temperature of 63°. A strong chorus formed the following night, after 0.83 inch of rain in the morning and with an evening temperature of 66°. Chorusing was still strong on May 6, and a few individuals called each night from May 7 through 12. Amplectant individuals were seen on the night of May 2. This pattern of rapid build up of choruses and spawning soon after heavy rain, followed by a dwindling off of calling activity, is fairly representative of the usual behavior in this species.

Activities in 1959 similarly showed strong relationship to rainfall. Heavy rainfall in mid-April (Fig. 2) failed to elicit calling possibly because it was accompanied by a sharp temperature drop that brought evening temperatures of 56° or below for a period of 7 days. A rainfall of 1.03 inches on May 22 brought no activity, but a moderate chorus formed after 0.88 inch on June 4. Heavy rains in late June, late July and late August were all followed by brief periods of strong chorusing, but very heavy rains in late September and early October elicited no activity.

Behavior in the wet year of 1957 differed considerably from the pattern discussed above. This was the year of the earliest start of calling (March 12), following a rainfall of 1.04 inches on March 11. A few individuals called on nights with evening temperatures of 60° or above in the period of March 11 through 19. Strong chorusing developed on March 21 and 22, following a rain of 1.64 inches on March 20. Following this, individuals could be heard on most nights through June 16, except as interrupted by temperature drops below about 60° evening temperatures. Not only was the calling season greatly drawn out in this wet spring, but the period of heavy chorusing was also extended. Strong choruses were heard from April 1 through May 2, except as limited by low temperatures. Spawning is known to have occurred on April 19 and 21, but this record is probably very incomplete. The number of calling individuals dropped greatly after May 2, but a rainfall of 3.26 inches on May 25 resulted in 3 nights of heavy chorusing. The approaching end of the calling season was evident on June 12, when 3.03 inches of rain resulted in only moderate choruses. The last calling of the season was heard on July 9, when several individuals called after a rainfall of 0.78 inch. Heavy rainfall on September 22-23 elicited no calling.

Four periods of strong chorusing in 1958 were associated with 4 of the 5 rains of approximately 2 inches or more that came in the warm season of that year. The last of these periods came on September 7, following a rainfall of 2.26 inches. Strong chorusing was heard on only the one night, but a few individuals called on the 2 following nights. No amplectant pairs were found in the local population in this period, but on September 7 a pair was found in a pool about 15 miles away. The 5th heavy rain of the season on September 19-20 resulted in calling by only a few individuals.

This is a warm-weather species that requires higher temperatures for calling than any others except *B. valliceps* and *R. catesbeiana* (Fig. 3). Most of the days on which calls were heard had evening temperatures of 63° or higher, up to 89°. Below this range, night-time calling was heard once with an 8 p.m. temperature of 57°, once with 59, and once with 60. The mating records were obtained on nights with evening temperatures of 66, 70, and 73° F.

Bufo valliceps

The reproductive activities of this population of the Mexican toad in relation to environmental factors have been reported in detail (Blair 1960) for a period that includes the first 3 of the 4 years of the present study, so no detailed treatment is required here. This species, with tropical affinities, has its calling limited by higher minimal temperatures than any other of the local anurans. The range of evening temperatures for calling is 65° to 95°, with a median of 80° (Fig. 3). Amplectant pairs were found at evening temperatures ranging from 66 to 89°, with a median of 77.5°. The peak of calling and spawning comes in spring, but summer breeding may occur after heavy rainfall. As in *R. pipiens* the same individuals (both males and females) are known to participate in both the spring and later breeding activities. Unlike the situation in *R. pipiens*, where the spring and fall reproductive activity is of approximately equal magnitude, the spring breeding of *B. valliceps* far exceeds any that may come later in the season.

The 1959 season was characterized by the correspondence between calling and spawning activities and heavy rainfall (Fig. 2), which is consistent with our previous evidence (Blair 1960).

DISCUSSION

The seasonal patterns of reproductive activity revealed in the preceding discussion are important in respect to their possible function as temporal isolating mechanisms and in respect to possible interpopulational competition.

Temporal isolation

The local complex of anurans includes 2 congeneric pairs of species. In both instances, the reproductive seasons of the congeneric species tend to come at different seasons, but both show considerable overlap. *Pseudacris clarki* spawns later and at higher temperatures than does *P. streckeri*, but there would be ample opportunity for hybridization if time of breeding were the only isolating mechanism. In all of the 4 years, male *P. clarki* called in the latter half of February, which is the peak of the spawning for *P. streckeri*, and *P. clarki* is known to spawn as early as February 4 (Lindsay 1958). There is then the possibility of reciprocal hybridization of the 2 species insofar as time of breeding is concerned, although this is minimized by the generally later breeding of *P. clarki* and by the habit of this species of breeding again in late summer and fall, when *P. streckeri* is absent from the breeding pools. There is little evidence as to when the local *R. catesbeiana* spawn, but the available information indicates that the peak of activity comes later than the winter-spring spawning season of *R. pipiens* and fails to overlap the fall season. There is great overlap in the calling seasons of the 2 species.

In both of the above instances, time of breeding seems to be one of the least important components of the isolating mechanism complex. Mating calls differ greatly in both pairs, and it has been shown experimentally that female *P. streckeri* discriminate between the calls of their own males and those of *P. clarki* (Littlejohn and Michaud 1959). Metamorphosis has been found in reciprocal crosses between the 2 species (Mecham 1957), but the hybrids have not been tested by backcrossing. No natural hybrid has ever been reported. The 2 species of *Rana* differ greatly in size as well as in mating call, and size alone would appear to be an effective isolating mechanism. Introgression of these species is blocked by genetic incompatibility, for Moore (1949b) has shown that the reciprocal hybrids fail at gastrulation.

Two species, *Acris crepitans* and *Microhyla olivacea*, have no near relatives in the local breeding complex. The situation is somewhat different with *Bufo valliceps*. Rare immigrants of 2 other species of toads (*B. woodhousei* and *B. compactilis*) have appeared at the pond, but neither has been able to establish itself there, and consequently these have not been considered in the present study. A distant chorus of *B. woodhousei* is heard each year somewhere to the southeast, and the nearest known population of *B. compactilis* is about 2 miles away on a different soil type.

Competitive relations

Interactions between species populations in respect to competitive relations would seem most likely in the larval stage, since individual *Bufo* and *Rana* lay several thousand eggs, and the others lay several hundred. No systematic sampling of the larval fauna of the breeding pools was done, but there is evidence to indicate the combinations of larvae that might occur at various seasons.

Larvae of the 2 species of *Rana* are in the pools virtually throughout the year. Two size classes of young *R. catesbeiana* were found in 1958. Several juveniles measuring from 65 to 113 mm in snout-vent length were marked in February and March, and a few additional bullfrogs of this age group were marked later that spring. These had to have been either the offspring of the 1957 breeding season, or immigrants, as the tank and all other local breeding pools dried up in 1956, with apparent extirpation of the local population. One freshly metamorphosed individual was marked on October 7, 1958, and possibly represented the earliest breeding of that same year. Two size classes of young bullfrogs were found in early 1959. Newly metamorphosed individuals were found on February 25 and March 7. Larger numbers of individuals representing a larger size class were marked in the period of February 17 (one of 55 mm) to August 4 (one of 68 mm). An individual with a snout-vent length of 56 mm was marked on February 2, 1960. The available evidence indicates that the larval stage lasts less than a year, but the exact duration remains to be determined.

The split breeding season of *Rana pipiens* results in there being larvae of this species in the pools throughout the year. Larval populations of the 2 species of *Rana* are therefore exposed to one another and potentially interacting in their demands on the pool environment throughout the year.

The temporal separation of their peaks of reproductive activity minimizes but does not completely prevent co-occupancy of the breeding pools by larval *P. streckeri* and *P. clarki*. The larval stage of *P. streckeri* apparently occupies about 6 weeks, which means that in most years the young of this species would have metamorphosed by the time the peak of *P. clarki* activity arrived. In 1957, spawning by *P. streckeri* was observed on February 13 and 24, and newly metamorphosed individuals were noted at the pond margin on March 27 and May 27. Those observed metamorphosing on the latter date presumably repre-

sented unnoticed spawning that occurred later than in February.

Larvae of *B. valliceps* and *M. olivacea* tend to be in the pools at the same times because of the dependence of these species on rainfall and on high temperatures. Both species spend approximately a month in the larval stage. In 1956, the laying of both species was largely confined to the nights of May 2 and 3, and newly metamorphosed individuals of both species were found at the pond margin on June 5. In 1957, *M. olivacea* was seen spawning on April 19-21, and newly metamorphosed individuals were noted on May 21. In 1957, the spawning of *B. valliceps* was greatly extended, but the peak came on April 2 to 7. Many metamorphosing toads were seen on May 23. Larvae of these species would also encounter those of *P. clarki* in the pools because of the similar season and habits of this species in responding to rainfall.

The larvae of *A. crepitans* are normally in the pools during the spring season, as judged from Pyburn's (1956) report, at which time they might encounter larvae of all of the other species, although the numbers of *P. streckeri* would be dwindling.

The broad picture may be generalized as follows. Ranid tadpoles of 2 species are using the pool environment throughout the year. There is considerable separation of the congeneric *P. streckeri* and *P. clarki* in the time their larvae are in the pools, but there is some overlap. Larvae of the latter species and the other opportunistic, warm-season breeders (*B. valliceps* and *M. olivacea*) tend to be in the pools at the same times. The greatest number of species and presumably the greatest biomass of tadpoles is found in the pools in spring.

SUMMARY

Nightly records of calling activity in a mixed population of 7 species of anuran amphibians near Austin, Texas, were kept over a 4-year period (1956-1959 inclusive) and records of spawning were also made. These records have been analyzed in relation to temperature and rainfall.

Pseudacris streckeri is a winter breeder. Calling begins as much as 2 months before spawning, which tends to be concentrated in late February. Rainfall is important in stimulating activity, and temperature largely determines periods of calling, although the threshold of limitation by low temperatures is lowered during the spawning season.

Pseudacris clarki calls and spawns later in spring than does its congener and differs from it in that there may be a 2nd period of activity in

late summer or early fall. The pattern of activity is a more opportunistic one in that choruses build more rapidly after rainfall and are more rapidly dispersed.

Rana pipiens has 2 clear-cut periods of major reproductive effort, one in winter-spring and the other in early fall. Calling but not spawning may continue through the summer. The wide range of temperatures under which spawning occurs accounts for the wide tolerance of temperatures reported for embryos of southern races of this species.

Rana catesbeiana has its calling activities largely limited to the hot summer season. This aquatic and littoral species does not form choruses in the pond, and its activities seem largely independent of rainfall.

Acris crepitans is largely limited to the environs of the breeding pool, and its activities are largely independent of rainfall. Spawning occurs in spring, although males continue to call through most of the summer. Late summer spawning may occur under special circumstances.

Microhyla olivacea is an opportunistic breeder that has its activities closely correlated with rainfall through the summer season. Spawning may occur from April to September.

Bufo valliceps is a late spring breeder that normally has its activities stimulated by rainfall. Its activities are inhibited by higher minimal temperatures than are those of any other of the local species. This species also shows opportunistic tendencies in breeding after heavy summer rains, but the summer activity is never equal to that of spring.

The diverse seasonal patterns or reproductive activity are of little importance as temporal isolating mechanisms in this situation, as most of the species are rather distantly related. The 2 congeneric pairs of species are largely separated by differences in spawning time, but in both there are other important isolating mechanisms. The diversity in time of spawning does tend to reduce the number and kinds of larvae in the pools concurrently and thus is possibly of significance in reducing competition at this life history stage.

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FACTORS INFLUENCING THE LOCAL DISTRIBUTION OF *MICROTUS* AND *SYNAPTOMYS* IN SOUTHERN MICHIGAN¹

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INTRODUCTION

Much of the information on local distribution of small mammals has been derived from faunal studies. Certain species are indicated to be most abundant in or absent from certain habitats. Detailed investigations of the physical and biotic factors present in habitats are few and the reasons for temporal and spacial variations in the local distribution of different species of small mammals are poorly understood.

Although some workers have studied biotic factors (Jameson 1949, Wetzel 1958), most of the studies to date dealing with the local distribution of small mammals have been concerned primarily with physical aspects of the environment. Thus, Shelford (1912) stressed the importance of physical factors and others have followed his lead (Chenoweth 1917, Green 1925, Hardy 1945, Chew 1951, Pruitt 1953 and 1959, Reynolds 1958). Much still remains, therefore, to be learned of the importance of biotic factors. Food supply, competition, and response to certain types of vegetation most surely influence the local distribution of many species.

To investigate the importance of biotic as well as physical factors under more or less natural conditions, a field study was made of the factors influencing the local distribution of small mammals in southern Michigan. The period of the study was September, 1957, through September, 1958. Data were obtained concerning *Microtus pennsylvanicus*, *Synaptomys cooperi*, *Sorex cin-*

ereus, *Blarina brevicauda*, *Peromyscus leucopus*, and *Zapus hudsonius*. This paper deals only with the first 2 species, the other 4 are treated elsewhere (Getz, in Press a and b).

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DESCRIPTION OF THE STUDY AREA

All work was done on the University of Michigan's Mud Lake Research Area in northern Washtenaw County, Michigan. The study consisted essentially of 3 parts, (1) a generalized study of 7 different habitats, (2) a more intensive study of 2 habitats (an abandoned field and a marsh), and (3) studies along a series of transects. A description is given only for the 4 habitats pertinent to the distribution of *Microtus* and *Synaptomys*. The transects have been described elsewhere (Getz, in Press a).

Old field

This is an abandoned field that was last planted to corn about 15 years ago. In the northern part

¹ A portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

of the field is a small depression that contains a refuse heap surrounded by *Salix* sp., *Populus tremuloides*, and *Cornus racemosa*. To the west is an outlet bordered by a narrow zone of sedges and *Solidago* sp. There are a few erratic boulders, up to a meter in diameter, on the surface. The soil is primarily sandy loam except in the low, moist sites which have a slightly higher humus content. Sheet erosion on the slopes has removed most of the top soil, leaving a sandy clay exposed. In comparison with the other areas, the old field is dry.

The vegetation consists primarily of *Poa compressa*, *Potentilla intermedia*, *Daucus carota*, and *Plantago lanceolata*. The surface is partly covered by a moss, *Brachythecium* sp. The eroded places have a sparse cover while the moist depressions support a more abundant growth of grasses.

Bog mat

This site, about 60 meters wide, along the northern side of Mud Lake, is a typical bog mat, relatively firm for the most part. The water level is usually 10 to 15 centimeters below the surface (in some places where the *Sphagnum* is absent it is at the surface). The very wet substrate is composed almost entirely of peat with very little mineral matter. There are 4 distinct plant communities present, (1) *Typha-Chamaedaphne*, (2) *Chamaedaphne*, (3) *Larix-Rhus*, and (4) *Carex-Scirpus*.

Spruce burn

This site is within a spruce stand that was burned about 27 years ago. Since the larger, older spruce trees are near the outer edge and the smaller, invading ones near the center, the area has a bowl-shaped profile. The habitat is characterized by a cover of *Sphagnum* and a uniform stand of leather-leaf (*Chamaedaphne calyculata*). The surface consists of hummocks of *Sphagnum* up to half a meter in height surrounding the bases of the leather-leaf. Between the hummocks the *Sphagnum* is only 10 to 15 centimeters thick. Below the *Sphagnum* is a humus substrate containing some mineral matter and charcoal, a remnant of the forest fire. The water table is .25 to .50 meter below the surface (depending upon the season). While the *Sphagnum* is relatively moist throughout the year, it is not as moist as that occurring in the bog. The hummocks in particular are relatively dry.

Marsh

The dominant plants in this habitat are sedges and grasses (for species lists see Getz 1959). One area contains primarily *Potentilla fruticosa*

and another a stand of *Solidago* sp. and *Aster* sp. There is considerable variation in species composition within the grass-sedge portion.

The surface is low with the water table usually only a few centimeters below the surface. During the wet season, water stands over most of the area. Only the portions that support the *Solidago*, *Aster*, and *P. fruticosa* were not inundated during the study. Of these the latter is on the higher ground (.50 to 1.0 meter above the general level of the marsh surface). The soil contains much fibrous, peaty humus and a moderate amount of mineral matter. The sedges and grasses grow from small hummocks 5 to 10 centimeters in diameter and height. The spaces between the hummocks are usually free of living vegetation. In the slightly drier portions these hummocks may not be completely submerged during the wet season. During the winter the dead vegetation falls over and forms a low canopy. Decaying vegetation also falls in between the hummocks to form a tangled mat that covers the surface. In the summer the vegetation completely covers the surface.

METHODS

Most of the methods have been described in detail elsewhere (Getz 1959, in Press a). Only those methods pertaining directly to *Microtus* or *Synaptomys* are given here.

For generalized study, a rectangular study area was established in each of the 4 habitats. Each study area, except in the burn area, contained 75 trap stations placed in a grid pattern with a 12-meter interval. The burn area was small and contained only 30 traps. The bog mat and burn areas were snap-trapped for 2 3-night periods (one trap at each station). Live-trapping data (see below) were utilized to get comparable information from the marsh and old field. The areas were trapped once in the fall (October and November, 1957) and again in the winter (January, 1958).

The entire old field (2.5 hectares) and a 4.4-hectare portion of the marsh were grided with a 12-meter interval. Both areas were live-trapped for 5 nights each month from September, 1957, through September, 1958. Because of the large number of stations in the marsh, 2 trapping periods were required to cover all of them. Live-traps of the type described by Burt (1940) were utilized. The traps were checked twice a day, 0800 to 1100 and 1600 to 1800. For dates of trapping see Getz (1959). Individuals were marked by toe clipping.

Mortality in the traps was low for *M. pennsylvanicus*. Of the 1128 individuals captured a total

of 6,412 times, only 74 (6.6%) died in the traps. Of 25 *S. cooperi* captured a total of 55 times, only 2 died in the traps.

For transect studies, a trapping station was established every 3 meters along each transect; one snap-trap was set at each station for 7 nights. The dates of trapping were 8 to 14 September 1958.

Studies of the environmental factors

Temperature

A temperature recording station was placed in each habitat studied. In the marsh and old field an additional thermometer was employed to obtain some specific comparisons of temperatures within the habitat. Each station contained 3 Max-Min thermometers which recorded temperatures one meter above, 2½ centimeters above, and 4 centimeters below the surface. The extra thermometers in the old field and marsh recorded surface temperatures. Taylor "Sixes" were used to obtain air and surface temperatures in all areas except the old field and marsh. Weston Max-Min dial thermometers (U. S. Weather Bureau type) were used to obtain surface temperatures in the old field and marsh as well as the subsurface temperatures in all areas. During the first half of the study the thermometers were read every other day. During the last half they were normally read only every 4 days, with a few readings every other day. The stations were normally visited between 1000 and 1400. Only the data from the level of the runways of the animals studied (surface strata of the marsh and old field and the subsurface strata of the bog and burn) have been included in this report.

Vegetation studies

Information was obtained concerning the amount of grass-like vegetation present, the species composition, and the physiognomy of each habitat studied.

Clip quadrats were employed to determine the amount of grasses and sedges present. The quadrats were established at scattered points throughout each area to sample those places that showed high or low population densities of *M. pennsylvanicus*. A square wooden frame with an inside dimension of one meter on a side was employed. Vegetation within the frame, regardless of where it was rooted, was clipped approximately 5 centimeters above the surface. The samples thus obtained were bagged, air dried, and separated by species for weighing.

Two series of such samples were taken from the marsh and old field, the first during the winter

aspect (early March) and the 2nd at the peak of productivity during the summer (June for the old field and July for the marsh). In all, 55 samples were taken in each series of clipping, 20 from the old field and 35 from the marsh. In addition, 5 samples were taken from each the bog mat, burn, and an oak-hickory upland adjoining the marsh in July.

Braun-Blanquet relevés (Dansereau 1957) were made in all study areas. These were used to determine species composition as well as to gain an idea of the physiognomy of the various habitats.

Moisture studies

Substrate moisture was determined by gravimetric methods. At various times during the year, 5 samples were taken from each area. A series was also taken from the old field in July for comparison of various portions of this area. Likewise, a series was taken from the marsh at its driest period (September, 1958) for a similar purpose. The water level at each trap station in the marsh was noted for each trapping period. These data were supplemented by observations on the location of the water table in the bog and burn areas.

Statistical analysis

Those data that lend themselves to statistical treatment have been analyzed by use of the Chi-square test and the Spearman rank correlation coefficient (Siegel 1956). In the following discussions the correlation coefficient (r_s) as well as the probability or level of significance (P) from Siegel (*op. cit.*) are given with statements of correlation.

RESULTS

Microtus pennsylvanicus

Vegetation

The results indicate that *M. pennsylvanicus* occurred only in grass-like vegetation as has been pointed out by numerous authors (Lantz 1907, Bailey 1900, Pearson 1959, and others). The generalized study and transect trapping showed it to occur only in situations in which the plants were predominantly graminoids—old field, marsh, and bog mat. Some *Chamaedaphne calyculata*, a woody plant, was present in the bog, but the captures were in areas in which this species was very sparse or absent.

The live-trapping data from the marsh verify the above conclusions (Table I). Of particular significance is the avoidance of the *Potentilla fruticosa* area. The vegetation of this area is composed predominantly of woody plants (*P.*

fruticosa). Interspersed with this species is a considerable amount of grass-like vegetation, as much as or more than the amount that occurs in the old field (Figure 1). *M. pennsylvanicus* almost completely avoided this area except when the population density of the rest of the marsh was at its higher levels (Figure 2). Even during the months of March and April, when members of the population were wandering the most (Getz, in Press c), few captures were recorded from the *P. fruticosa* area.

TABLE I. Analysis of captures of *Microtus pennsylvanicus* from different vegetation types in the marsh. $\chi^2 = 1020$; $P = < .001$

Vegetation type	No. of traps	No. of captures	Average captures per trap	Expected No. captures*
Woody**	16	7	.4	334
Woody plus grasses and sedges	38	147	3.9	794
Forbs	7	50	7.1	146
Forbs plus grasses and sedges	19	408	21.5	397
Grasses and sedges	194	5110	26.3	4051

* If distribution is random.

** Includes data from Getz, 1960a.

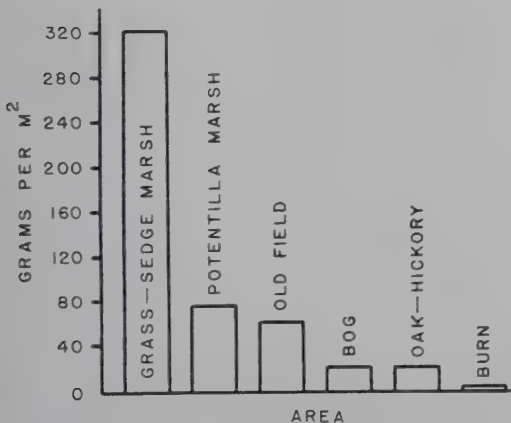


FIG. 1. Standing crop of graminoids. Determined from clip quadrats taken at the peak of productivity.

Wooded areas were also avoided by wandering individuals (Table I). Only 4 captures were recorded during the entire year for 4 traps located in a *Cornus racemosa* stand although stations immediately adjacent to the area recorded up to 25 captures. In a small, 0.2-hectare oak-hickory upland within the study area in the marsh, only

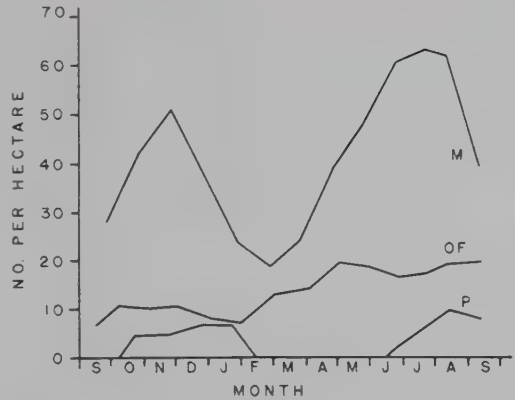


FIG. 2. Population densities of *Microtus pennsylvanicus*, September, 1957, through September, 1958. M, grass-sedge marsh; OF, old field; P, *Potentilla fruticosa* marsh.

2 captures of "wandering" *M. pennsylvanicus* were recorded during the entire study period (Getz 1960a). Numerous captures were recorded, however, in adjoining stations in the marsh. Only one capture was recorded in a small stand of *Spiraea* sp. (about 10 meters in diameter). Complete data for each trapping period are given by Getz (1959).

A larger oak-hickory island in the marsh has one portion containing as much grass-like vegetation as the bog (Fig. 1), but no *M. pennsylvanicus* was captured there. No woody "barrier" was present; the site was continuous with the surrounding marsh.

There was an avoidance of areas containing only forbs. Seven traps in the marsh were located in pure stands of forbs and these were in all cases immediately adjacent to grass-like vegetation. Nevertheless, *M. pennsylvanicus* captures were significantly fewer in these traps than in those located in vegetation consisting of both forbs and grass-like plants (Table I). The areas that had considerable amounts of *Solidago* and *Aster* in addition to the grass-like vegetation gave no indication of being avoided by *M. pennsylvanicus*. Captures in these places were only slightly lower than where the vegetation was entirely grass or sedges. This is interpreted below as a reaction to the amount of grass-like vegetation present. In one portion of this type more captures were recorded per trap (35) than the average captures per trap for the grass-sedge area (26.3). The places where the grasses and sedges were sparse were sufficient in size to give an impression of avoidance of the forb-grass-sedge type.

No evidence indicated that *M. pennsylvanicus* selected any particular species of grass or sedge.

Several small uniform stands of one or 2 species of grasses and sedges occurred in places within the marsh. Although they are too small to be submitted to statistical analysis, there was no noticeable selection or avoidance of any particular species.

During the June trapping period a line of 12 live-traps (spaced 12 meters apart) was placed in a portion of the marsh adjoining the study area. The water depth was 2 to 5 centimeters and the vegetation was estimated to be as abundant as in the main study area. The sedges had a growth form of uniformly spaced shoots, not clumps as in the main study area. No *M. pennsylvanicus* was taken in these traps in 5 days of trapping. While such a small amount of sampling does not necessarily indicate complete avoidance of the area, it does indicate a lesser abundance than in the remainder of the marsh. This may result from the growth form of the vegetation. Nests and feeding stations would be more difficult to construct here than in the area in which the vegetation grows in clumps.

Cover

Although cover is commonly a vague term implying such things as protection from predation and modification of extremes of sunlight, temperature, and moisture, it can, in the case of *M. pennsylvanicus*, be applied more specifically to that particular physiognomic type of vegetation that is most suitable for the construction of this animal's characteristic system of runways. Since the vegetation serves as food as well as cover it is difficult to evaluate the one function separately from the other. Eadie (1953) and Mossman (1955) have found indications that the relative abundance of *M. pennsylvanicus* may be related to the amount of grass-like vegetation present.

In determining responses to the amount of cover, correlations were obtained between the distribution of *M. pennsylvanicus* and the total amount of cover, including the dead debris on the ground as well as with the living vegetation. The latter measure is a better estimate of the cover, especially in the marsh. In this area much of the dead material was below the water when the marsh was inundated and thus offered no cover at such times. That portion of the living vegetation that was clipped was above the water and thus gives a better comparative estimate of the cover. Unless otherwise indicated, the cover afforded by the living vegetation (dry weight) has been used in the following discussions.

When making comparisons between the areas there was evidence of a definite relationship be-

tween the abundance of *M. pennsylvanicus* and the amount of vegetation (cover) present. Clipping data showed the amount of grass-like vegetation in the marsh, old field, and bog to be in the proportion of 13:2.5:1, respectively. Data obtained from the generalized study revealed the relative density of *M. pennsylvanicus* in the same areas to be practically the same (13:3:1).

Live-trapping in the old field also revealed some evidence of a correlation between the amount of vegetation present and the number of captures (March data: $r_s = .39$; $P.05 = .399$; July data: $r_s = .72$; $P < .01$). Comparisons of the number of captures with the amount of graminoid vegetation present at various places within the forb-grass-sedge marsh show that the fewer captures occurred where there was a lesser amount of grasses and sedges ($r_s = 1$; $P < .01$).

The almost complete absence of *M. pennsylvanicus* from the *P. fruticosa* area does not appear to result from the paucity of grass-like vegetation. Although such vegetation did occur in less abundance here than in the remainder of the marsh, there was more than in the old field, which supported much higher *M. pennsylvanicus* population densities (Fig. 2). While this lesser amount may be involved, the woody nature of the dominant plant appears to be the primary factor.

During the early winter (November to December) several individuals in the marsh moved out of an area that supported very little grass-like vegetation and into places that supported a more abundant growth. However, no correlation between the amount of dead vegetation present and abundance of *M. pennsylvanicus* was observed during the winter (Feb: $r_s = -.02$; March data: $r_s = -.22$; $P.05 = .343$). During the remainder of the year there was also no correlation between amount of vegetation present and abundance of *M. pennsylvanicus* in the grass-sedge portion of the marsh.

Food

Grasses and grass-like plants constitute the normal food items for *M. pennsylvanicus* and may be a primary factor in its restriction to certain habitats. Observations of clippings at feeding stations revealed that this species was feeding on all species of grasses and sedges present. Of the forbs, only *Impatiens capensis* was observed to be eaten. During the winter the succulent shoots at the bases of the sedges (within the bases of the dead leaves) were eaten.

The clipping data revealed that there was sufficient food in all areas to support much larger populations than were attained during the course of

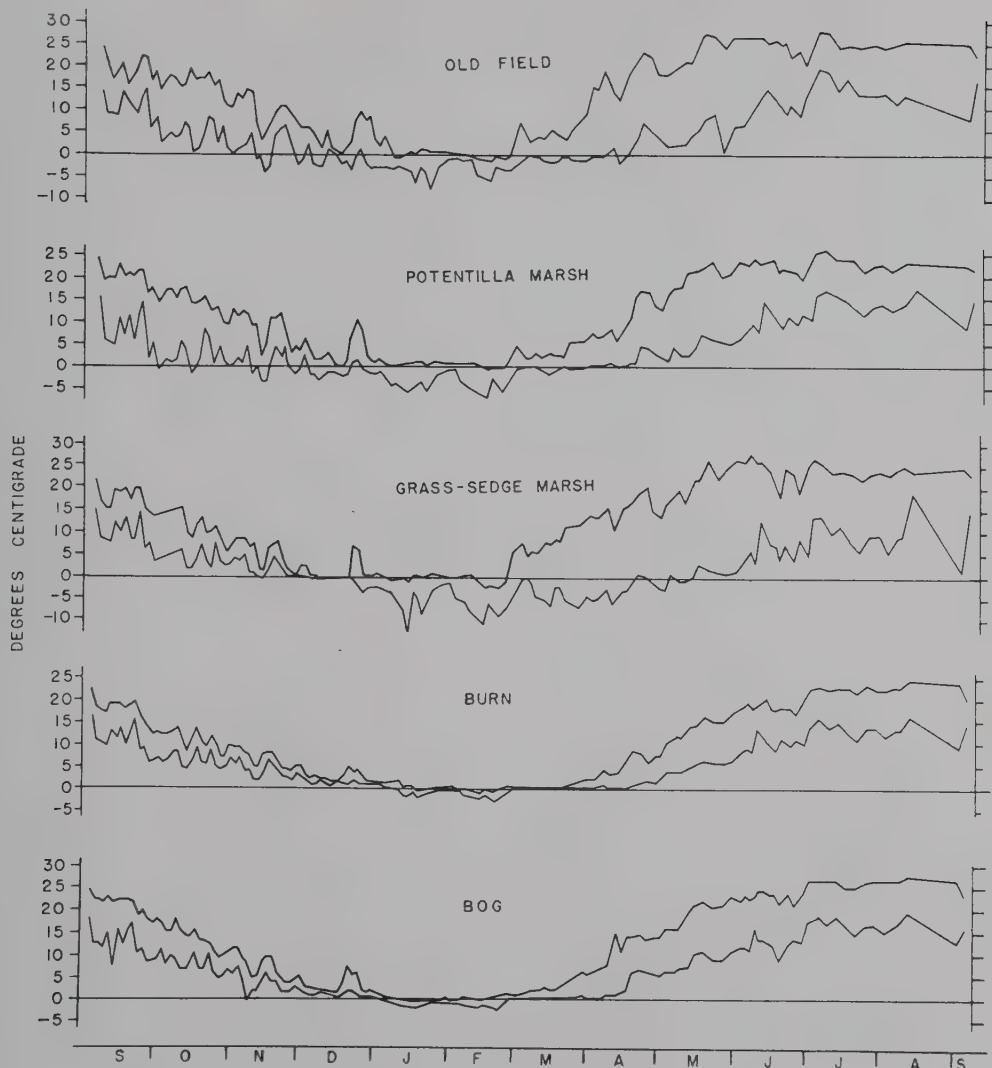


FIG. 3. Maximum and minimum temperatures, September, 1957, through September, 1958. Surface temperatures are given except for the bog and burn. Substrate (4 cm deep) temperatures are given for these 2 areas.

the study. The amount of available food, therefore, does not appear to be a primary factor in the local distribution of *M. pennsylvanicus*. The type of food (graminoids) does appear, however, to be a major factor responsible for its occurrence in grassy areas.

Temperature

Elton (1942), citing Sviridenko, suggested that *Microtus* may be more susceptible than other small mammals to temperature extremes. If this is true, temperature could exert an influence upon

the local distribution of *M. pennsylvanicus*. However, I know of no studies of temperature stress in this species.

Temperatures at the level of the runways where *M. pennsylvanicus* is active are relatively mild and uniform (Figure 3). It is true that surface temperatures are sometimes more extreme in areas that have no herbaceous vegetation (e.g., some forest habitats) than they are in areas where the vegetation is primarily herbaceous. However, one portion of the old field in which *M. pennsylvanicus* was abundant displayed temperatures that

were as extreme as any non-graminoid area studied (e.g., spruce swamp, hardwood swamp, and oak-hickory upland; Getz, in Press a). Behavioral responses to the extremes in temperature were noted in the old field, however.

M. pennsylvanicus was not more abundant in the areas displaying the more nearly uniform temperatures. Temperatures were more uniform and mild in the bog than in any other habitat in which this species occurred, but it was least abundant here. The temperatures of the portions of the old field that supported the denser stands of vegetation were milder than those of the grass-sedge marsh, but they supported fewer *M. pennsylvanicus* than did the marsh. Likewise, the *P. fruticosa* area of the marsh, in which *M. pennsylvanicus* was scarce, displayed more moderate temperatures than the grass-sedge portion where it was most abundant. One of the sites in the old field in which it was as abundant as anywhere else in this area had summer temperatures that averaged about 7° C higher than where it was not so abundant; this site also probably had extremely low temperatures during the winter months (data were obtained only during the summer). Temperature, therefore, obviously was not an important factor in the local distribution of *M. pennsylvanicus*.

In the old field, modification of the activity pattern resulted from responses to temperature extremes. During the months in which extremely low temperatures prevailed, almost no captures were made. Thirteen *M. pennsylvanicus* that resided on the area during this period were not captured. They apparently stayed in the mole burrows in which their nests were located and foraged for only very short distances. In summer, when temperatures were high, relatively fewer captures were made during the day than in months when the daytime temperatures were more moderate. The marsh showed similar indications, but these were much less marked as there was more vegetation and moisture present to reduce the temperature variations.

Humidity and/or available free water

That *M. pennsylvanicus* is often abundant in moist situations (even in areas that are seasonally inundated) is well documented (Lantz 1905, 1907, Gunderson 1950, Schmidt 1931). Such situations frequently support a dense stand of grasses and sedges, and in these cases there occurs an interaction of the associated factors of moisture and vegetation.

The generalized study showed both the high and low abundances in wet areas (marsh and bog,

respectively). This indicates that moisture alone is not the dominant factor in the local distribution of *M. pennsylvanicus*.

Live-trapping data from the marsh revealed a slightly greater number of captures from those stations that had 2.5 to 10 centimeters of standing water around them than from those with no standing water or with 12.5 or more centimeters of water (Table II). There was a direct correlation between the amount of graminoids and the depth of standing water (Getz 1960b). When the influence of vegetation is eliminated there appears to be a slight avoidance of standing water. No relationship was apparent between the actual depth of water and utilization of the area, however.

TABLE II. Relation of captures of *Microtus pennsylvanicus* to depth of water. Data represent compilations for all months standing water was present on the area

Average water depth (cm)	No. of traps	No. of captures	Average capture per trap (5 days)
0.....	415	828	2.0
2.5.....	217	626	2.9
5.0.....	100	266	2.7
7.5.....	38	102	2.7
10.0.....	63	157	2.5
12.5.....	28	34	1.2
15.0.....	51	66	1.3

As long as some vegetation was present above the surface where the nests and feeding stations could be constructed, standing water was not completely avoided. Observations in a cattail marsh adjoining the study area were made to add to these data. From these observations it was seen that *M. pennsylvanicus* occurred where there was 50 to 60 centimeters of water. In these places only the tops of the clones of sedges were above water. Numerous small feeding stations were constructed in these clones at the waterline. Fresh clippings and droppings were abundant, an indication of large numbers of *M. pennsylvanicus* in the area. Data regarding the movement of individuals in the marsh revealed no indication of animals moving from a drier site to an inundated one after a rain. Neither was the opposite movement observed.

No correlation existed between soil moisture and the occurrence of *M. pennsylvanicus* when standing water was absent from the marsh (September, 1958 data: $r_s = -.12$; $P.05 = .425$). A slight correlation existed between the substrate moisture and number of captures in the old field (July, 1958 data: $r_s = .59$; $P < .05$).

Interspecific competition

Findley (1954) has shown competition to be a factor influencing the local distribution of *M. pennsylvanicus* in regions where other species of the genus also occur. No other species of *Microtus* occurs in southeastern Michigan, but other species of small mammals that possibly could compete with *Microtus* were present. During the winter, 24 *Peromyscus leucopus* moved into a small portion of the marsh. Most of these animals remained there from December through March. During this time the same portion had as high a population density of *M. pennsylvanicus* as any other part of the marsh. The presence of the *P. leucopus* had no apparent influence upon the *M. pennsylvanicus*.

Stations in both the marsh and old field that yielded numerous captures of *Zapus hudsonius* and/or *Synaptomys cooperi* also recorded numerous captures of *M. pennsylvanicus*. These 2 species apparently had little influence upon the local distribution of *M. pennsylvanicus*.

Predation

Several papers report predation on *M. pennsylvanicus* by the short-tailed shrew, *Blarina brevicauda* (Eadie 1944, 1948, 1952, Barbehenn 1958, Schmidt 1931). Barbehenn (*op. cit.*) believed that *B. brevicauda* may influence population levels of *M. pennsylvanicus*, but found no evidence that the local distribution is affected by shrew predation.

The higher *Blarina brevicauda* population densities in the marsh were recorded in the *P. fruticosa* area. However, this does not seem to be a factor in the smaller numbers of *M. pennsylvanicus* in this area. During the month of April when the shrew population was at a low (and movement of *M. pennsylvanicus* at a maximum) no increase in the captures of *M. pennsylvanicus* in this area was noted. Only when the population densities were higher, resulting in more population pressure in the grass-sedge area, did the number of captures increase in the *P. fruticosa* area (Fig. 2). At other stations in the marsh and in the old field both species occurred in abundance.

Synaptomys cooperi

The bog lemming, *Synaptomys cooperi*, is found in grassy areas, particularly in moist situations (Burt 1948, Howell 1927). Hamilton (1941) found it to be locally abundant also in a beech-hemlock stand and Connor (1959) found it in areas containing woody vegetation. *S. cooperi* is similar to *Microtus pennsylvanicus* in that both inhabit grassy areas, especially in moist

situations, and occupy surface runway systems formed under the vegetation. Both utilize grass-like vegetation as a primary source of food.

The limited data obtained concerning *S. cooperi* were sufficient to determine the areas they inhabit and thus permit a few general conclusions and some comparisons with *M. pennsylvanicus*.

Vegetation

S. cooperi was found only in areas containing grass-like vegetation. The presence of woody plants apparently did not influence its local distribution. In the marsh it was more abundant in the *P. fruticosa* area than in the purely grass-sedge type. The transect data also showed it to occur where *Chamaedaphne* and *Vaccinium* were present.

Moisture

S. cooperi occurred primarily in moist or wet (marsh, bog, and burn) situations with only 4 captures in the drier old field (compared with 51 in the marsh). Moisture, therefore, appears to be an important factor in its local distribution, perhaps even more so than in the case of *M. pennsylvanicus*. In the marsh it appeared to avoid standing water, thus differing somewhat from *M. pennsylvanicus*.

Temperature

The conclusions regarding *M. pennsylvanicus* also apply to *S. cooperi*. The runways are well sheltered from extremes in temperature so that temperature would have little influence over its local distribution. Insufficient data were obtained to substantiate this conclusion.

Interspecific competition and predation

In the marsh, *S. cooperi* was most abundant in the *P. fruticosa* area which was avoided by *M. pennsylvanicus*. However, it was relatively abundant at other stations where this latter species was also abundant, so competition does not appear to be the main factor. Since *Blarina brevicauda* was also quite abundant in the *P. fruticosa* area, *S. cooperi* did not appear to be influenced in its distribution by this species.

CONCLUSIONS AND DISCUSSION

Although similar in some of their habits, the present study has indicated differences in the ecology of *S. cooperi* and *M. pennsylvanicus*. The type of vegetation appears to be the most important factor influencing the local distribution of both species. Since graminoid vegetation is utilized as the primary source of food and their characteristic runway systems are most easily

constructed in this type of vegetation, areas supporting graminoids are selected over others. While both occur only in those areas containing grass-like vegetation, *S. cooperi* is not influenced by the presence of a considerable amount of woody vegetation, situations which *M. pennsylvanicus* avoids. This avoidance of woody vegetation has not been explained. *P. fruticosa* (which was avoided) has a physiognomy similar to low forbs. The actual factors involved may, therefore, be rather subtle.

Although both species require moist habitats, *S. cooperi* appears to require more moisture than *M. pennsylvanicus*; it also avoids standing water where the latter species may be abundant. It is possible that both species have a high evaporative loss of moisture so that water loss becomes too great in the drier situations to maintain a proper water balance (Lindeborg 1952, Getz unpublished). The positive response to moist situations and greater amounts of cover may, therefore, result from higher humidity. This needs to be investigated further.

There is no evidence that temperature is a major factor in the local distribution of either species. Variations between the different types of habitats in which they occur are slight. In this study *M. pennsylvanicus* was actually most abundant in an area having more extreme temperatures. Data from the other grassy areas as well as from the wooded areas also failed to show any relationship between temperature and local distribution. At times of the year during which extreme conditions exist (*i.e.*, winter and summer) behavioral responses such as modification of the pattern of activity may occur so as to allow the animals to avoid these extreme conditions while remaining on the area.

It, therefore, appears that biotic factors (*i.e.* type of food and vegetation) are as important in regard to the local distribution of both *M. pennsylvanicus* and *S. cooperi* as are the physical factors of the environment. Only within areas that have favorable types of food and vegetation do the physical factors influence local distribution. In the areas of the present study moisture was the only physical factor that exerted noticeable influence upon these 2 species.

SUMMARY

A 13-month study was made of the factors influencing the local distribution of *Microtus pennsylvanicus* and *Synaptomys cooperi* in southern Michigan. The small mammal distributions were determined by snap-trapping 2 habitats (bog mat and burn area) at 3 different times and by month-

ly live-trapping of a marsh and abandoned field. The environmental factors studied were vegetation, food, temperature, moisture, cover, and interspecific competition.

Both species, owing to their dependence upon graminoids as a source of food, were found only in areas having grass-like vegetation. *M. pennsylvanicus* avoided grassy areas containing woody plants; *S. cooperi* did not avoid such situations. There was a positive correlation between amount of graminoids and abundance of *M. pennsylvanicus*. This appeared to be a combined influence of a greater food supply and increased humidity resulting from the greater cover. Temperature exerted no influence upon either species. In places where the temperature conditions were most extreme, behavioral responses occurred that permitted *M. pennsylvanicus* to avoid the extreme conditions while remaining on the area. Moist situations were preferred over drier ones. This may be related to an inability to adjust body losses of water. Standing water was not avoided by *M. pennsylvanicus* so long as vegetation was present above the surface in which nests and feeding stations could be constructed; *S. cooperi* avoided standing water. Interspecific competition and predation by shrews were not important factors influencing the local distribution of either species.

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A STUDY OF CHARLESTOWN AND GREEN HILL PONDS, RHODE ISLAND¹

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The south shore of Rhode Island is characterized by a number of shallow, usually brackish embayments known as "salt ponds" by the local inhabitants. Certain of these ponds are highly productive of marine crops and others are relatively barren. Charlestown Pond and Green Hill Pond were chosen for study as a convenient contrast between the highly productive and relatively unproductive types.

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GENERAL DESCRIPTION OF THE ENVIRONMENT

The Charlestown-Green Hill Pond system is situated in southern Washington County, Rhode

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Island about 6 miles west of Point Judith. Charlestown or Ninigret Pond is 4 miles long with a surface area of about 1560 acres. Adjacent on the east is Green Hill Pond, about one mile across and with 420 acres of surface. There is a 100-foot beachway protected by stone jetties connecting the eastern end of Charlestown to Block Island Sound, but Green Hill has no access to the outside except through the narrows into Charlestown Pond. The effluents of Cross Mill Pond and King Tom Pond enter the northward extension of Charlestown known as Fort Neck Pond. In addition there is appreciable ground water entering along the northern shore. Factory Pond Brook and a nameless smaller stream, which enter the northern cove of Green Hill Pond, constitute the principal remaining sources of fresh water to the pond system. Figure 1 illustrates the bathymetry and general topography of the environment.

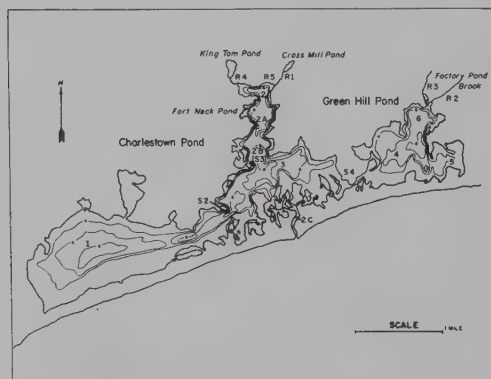


FIG. 1. Bathymetry and topography of the Charlestown-Green Hill Pond system with location of sampling stations. Depths in feet. See Table I for brief description of each station.

These ponds are submerged outwash plains formed along the edge of the Harbor Hill moraine and subsequently cut off by baymouth bars (Johnson 1925). In Rhode Island almost none of the outwash plain remains above sea level and the edge of the moraine forms the irregular northern shore of the ponds (see Fig. 1). Presumably Charlestown and Green Hill Ponds were one continuous embayment at an earlier period and indeed they are often figured as such in early charts of the Rhode Island shore. With the shoreward advance of the barrier beach the connection between the ponds has become increasingly restricted until today it is a shallow tidal river.

The bottom sediments within the ponds are of 3 distinct origins reflecting the geological history

of the ponds and the dynamic forces presently operating in them (Dr. R. L. McMaster, personal communication). The deposits along the northern shore are largely an unsorted mixture of cobble, gravel, and coarse sand of glacial origin. Extending into the ponds from the barrier beach is an extensive tidal delta of well sorted sand. The sediment in the central portion is principally silt containing considerable organic matter presumably resulting from organic production within the ponds.

RECENT HISTORY OF THE PONDS

It is certain that the life of a salt pond is relatively short in geological history, but at present there is little information concerning the chronology of events during the formation and eventual elimination of such an environment. Because Charlestown Pond was once a commercial harbor of some importance and long has been economically important on account of its shell fisheries, there is some recorded history, dating back over 300 years, which provides information about the timing of recent events within this environment.

It is known that the Dutch occupied the area at the head of Fort Neck Pond about 1630 (Goodwin 1932) and presumably traded with the Indians. At this time the inlet was certainly navigable to the sailing ships of the day (Bradner 1921), but it had begun to close by 1734 when the General Assembly of the Colony appointed a committee to consider diverting the Pawcatuck River into Fort Neck Pond to keep the harbor open (Bartlett 1859). By 1752 the inlet could no longer be used as a harbor and the subject of diverting the Pawcatuck was again brought before the General Assembly since "there was no harbor . . . between Dutch Island (in Narraganset Bay) and Westerley." In 1761 an Act was passed in the General Assembly to establish a lottery to raise £20,000 for the work though apparently nothing was actually done. The problem of silting of the inlet was frequently referred to at legislative assemblies during the remainder of the 18th and the 19th century but it was not until 1904 that a 60-foot breach with stone jetties was built. This did not eliminate the problem, and in 1952 the present 100-foot "protected" breach was constructed by the State Division of Harbors and Rivers. Comparison of aerial photographs taken in 1952 before the new breachway was completed and again in 1954 demonstrates the rapidity with which the increased tidal force and increased sediment load are decreasing the volume of the already rapidly disappearing pond.

METHODS OF INVESTIGATION

Sampling

At the outset of the study, 6 stations were established in the ponds to be sampled weekly, weather permitting, for salinity, temperature, oxygen, inorganic phosphate, chlorophyll, and zooplankton. Three additional stations were regularly sampled for surface salinity and temperature. It became evident as the program developed that certain stations were less significant than others and that weekly sampling presented an impossible analytical burden with the personnel available. During the 2nd year of the study nitrate analyses were undertaken, bimonthly sampling instituted, and, at this time, stations 5 and 6 in Green Hill Pond were virtually eliminated from the program. In the fall of 1957 three additional stations were visited to enable more intensive study along the north-south salinity gradient in Charlestown Pond. On a few occasions samples of water from fresh water effluents were also collected. The location of all

stations is shown in Fig. 1. A brief description of each station with the number of times sampled is contained in Table I.

Surface water samples were usually taken in glass jars of one- or 2-quart capacity dipped over the side of the skiff. For sub-surface samples the jar was inserted in a weighted wooden box fitted with a water-tight rubber gasket which could be opened at any desired depth and closed again by means of an attached cod line. Zooplankton collections were made with the Clarke-Bumpus sampler and a #12 bolting cloth net.

Sampling was carried out from an outboard-powered skiff normally within a period of 4 to 5 hours. Samples were returned to the laboratory immediately, refrigerated, and analysis carried out the day following. Correlative meteorological data for any sampling dates were obtained from U. S. Weather Bureau's monthly report, "Local Climatological Data" collected at Providence and Block Island. Information on daily solar radiation was supplied by the Eppeley Experimental Laboratory in Newport, Rhode Island.

Analyses

Temperature measurements were made by inserting a bucket thermometer in the glass vessel used to collect water samples as soon as it was brought aboard.

Salinity was determined with Weksler hydrometers as soon as the water samples were returned to the laboratory. Comparison of duplicate samples with the hydrometers and silver nitrate titration over a salinity range from approximately 4 to 30 ‰ suggested a systematic error of about + 0.5 ‰ for the hydrometer values which was not considered significant in view of the highly variable salinities encountered in the ponds. Since all the salinities were determined in the same manner, they should be comparable among themselves.

Because the ponds are shallow and contain relatively little suspended matter, the Secchi disk could not be used to obtain a measure of transparency. Alternatively an extinction coefficient per meter was determined for each water sample with the Klett-Summerson photoelectric colorimeter using the Klett 66 red filter and the 4 cm cell. Riley (1956) gave the formula

$$K = 0.96 K_1 + 0.246 \quad (1)$$

relating K determined from Secchi disk readings to K_1 the extinction coefficient obtained by means of the Klett. This formula was used to obtain an extinction coefficient K for samples from the salt ponds.

TABLE I. Description of stations with frequency of sampling

Station	Mean depth (ft.)	Remarks	No. occasions sampled
1	6	Conditions relatively uniform; over sandy bottom supporting principally low-growing attached algae	52
2	5	Varying salinities; frequent salinity stratification; soft bottom supporting dense stand of <i>Ruppia maritima</i>	52
3	5	Generally high salinity; soft bottom; dense <i>Zostera marina</i> with "aufwuchs" of algae	51
4	5	Brackish; very soft bottom with almost no vegetation	52
5	4	Brackish; very soft bottom with little vegetation	22
6	3	Very brackish; very soft bottom with little vegetation	21
2A	7	Deepest station; frequent salinity stratification; soft bottom; mixture of <i>Zostera marina</i> and <i>Ruppia maritima</i>	5
2B (S3)	6	High salinity; sandy bottom with some <i>Zostera marina</i> present	6
2C	Variable	In breachway channel on flood tide or from B.I.S. ½ mile from breach on ebb tide; high salinity; much suspended matter	9
S2	8	Salinity and temperature samples only; generally high salinity	49
S3	6	Salinity and temperature samples only; same description as 2B	47
S4	3	Salinity and temperature samples only; variable salinity; rapid tidal current	48
R1	1	Cross Mill Stream; principal tributary to ponds; clear stream, sandy bottom; pH 7.2	12
R2	½	Factory Pond Brook; slightly stained with humic substances; marshy bed; pH 7.1	5
R3	1	Drains small pond; slightly stained with humic substances; pH 7.0	5
R4	½	King Tom Stream; slightly stained with humic substances; flow, controlled by dam, variable	3
R5	—	Springs along edge of moraine; clear; little seasonal temperature change	3

Oxygen was measured by the Winkler method and percentage saturation values determined from the nomogram prepared by Richards and Corwin (1956).

Samples for inorganic phosphate determination were preserved with a few drops of reagent grade chloroform and refrigerated overnight before analysis. The molybdenum blue method as modified by Wattenberg (1937) was used for the determinations except that it was found desirable in these highly variable pond waters to standardize every sample as suggested by Harvey (1955). The Klett-Summerson photoelectric colorimeter with filter K66 (red) was used to measure the intensity of color developed.

The method of Mullin and Riley (1955) was used to determine inorganic nitrate except that a Klett with filter K54 (green) rather than a spectrophotometer was employed. Since it is necessary with this method to filter the water before analysis, the filtrate from the chlorophyll samples was usually taken for nitrate determination.

Chlorophyll was estimated using the method described by Riley and Conover (1956). Only chlorophyll *a* values were recorded.

The estimation of zooplankton displacement volumes presented a special problem because of the small size of many of the samples. The #12 net hauls were of short duration to prevent excessive contamination of the samples with plant material after the net had begun to clog. The following method proved most satisfactory. The plankton sample was filtered onto #25 bolting cloth using mild suction. It was found helpful to pour the sample down a glass rod to keep it concentrated in the center of the cloth disk. The bolting cloth was then placed on a glass plate, sample side up, and the plankton carefully scraped off with a spatula and rubber policeman. The material on the spatula was then washed into a 5 or 10 ml graduated cylinder with water from a 10 or 25 ml burette. The total volume in the graduate cylinder less the volume of water used in washing was equal to the displacement volume. With this method total volumes less than 0.1 ml could be determined with some precision.

SEASONAL CYCLES AND REGIONAL DIFFERENCES IN CERTAIN ENVIRONMENTAL VARIABLES

As the investigation of the salt ponds proceeded, it became clear that the environment was made up of at least 4 regions, each topographically, hydrographically, and biologically distinct but not completely independent of the others. The breachway to Block Island Sound opens into the

central basin (station 3). To the west lies a large, partially isolated basin receiving very little land drainage (station 1). To the north extends a level-bottom, steep-sided valley, Fort Neck Pond, receiving about half of the total fresh water drainage (station 2). On the east, Green Hill Pond is completely isolated from the remainder of the system except for the narrows and it receives the remaining land drainage (station 4, also 5 and 6). (See Fig. 1 and Table I for a more complete description of these 4 regions.) Therefore, it will be necessary to consider the seasonal cycle of events in the different sections before turning to problems pertaining to the system as a whole.

Distribution of temperature and salinity

The seasonal distribution of temperature and salinity for stations 1-4, shown in Figure 2, serve to illustrate certain characteristic features of the different portions of the environment. The seasonal temperature range of 0-26° C was approximately the same for each station but the vertical distribution on any given date was seldom the same. Despite the shallow water column, a weak thermocline was commonly observed during the warmer months at stations 2 and 3, occasionally at station 4, and almost never at station 1. The vertical distribution of salinity clarifies in part the reason for these differences in stability. The vertical gradient was slight in the western basin (1), usually less than 2 ‰ though occasionally much more in Green Hill Pond (4), but at stations 2 and 3 a halocline was virtually always present. The range of salinity at station 1 in the western basin varied only slightly from week to week, reflecting the small amount of runoff entering this section and suggesting that both horizontal and vertical mixing were appreciable. Since about half the total runoff enters the ponds along the north shore of Fort Neck Pond, there were variable surface salinities at station 2. There would seem to be a net surface transport down Fort Neck Pond toward the breach resulting in lower salinities in the surface waters at station 3 as well. A tongue of more saline water from Block Island Sound underlaid the brackish water at station 3 and extended up the cove to station 2. Both surface and bottom salinities showed short term variations in Green Hill Pond but not necessarily in the same direction. The isolated position of this basin makes it highly susceptible not only to variation in runoff but also to tide and wind effects controlling exchange over its shallow sill.

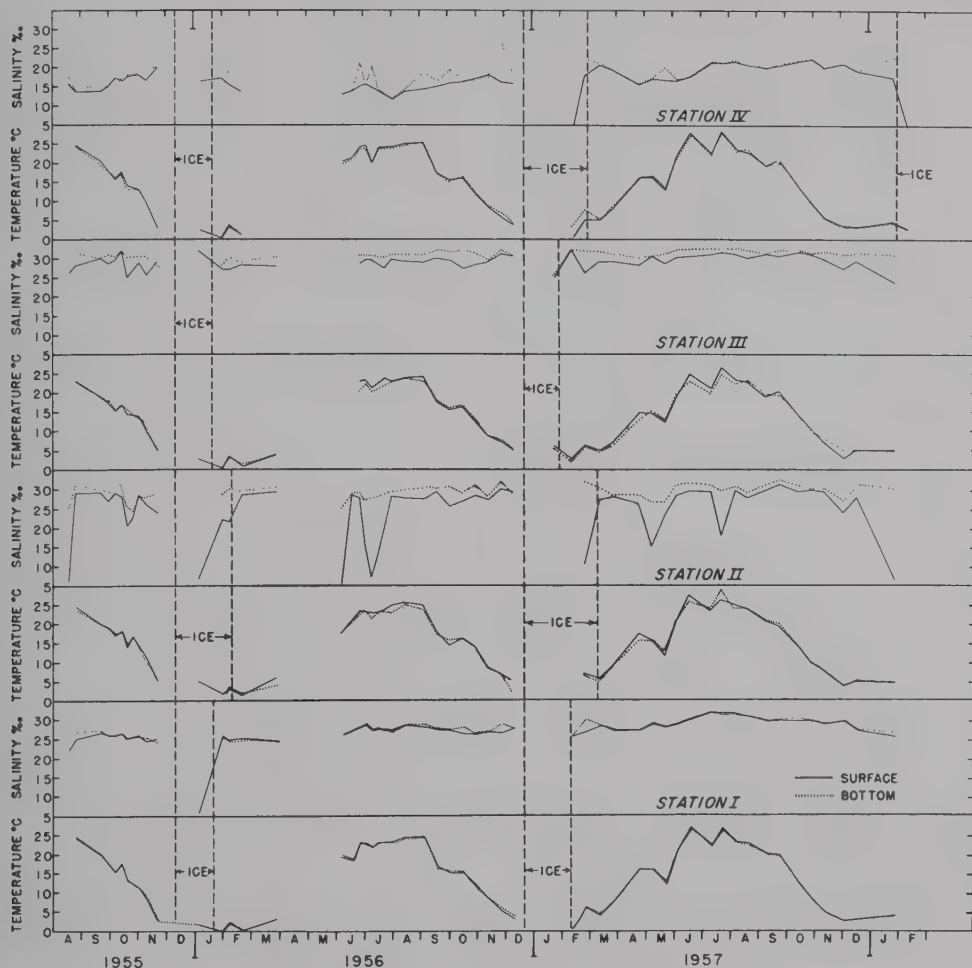


FIG. 2. Seasonal distribution of temperature and salinity at stations 1-4.

Unsuccessful attempts were made to find statistical correlations between bottom salinities in Green Hill and in the western basin and the prevailing wind direction and phase of the moon. However, it is almost certain that tide and wind are in large measure responsible for the variability in salinity in the more isolated basins.

Two deficiencies in the data may be responsible for the lack of statistical verification. In the first place, the nearest meteorological station providing information about the wind direction and intensity is at Providence some 30 miles inland. The vagaries of wind in the vicinity of water are well known. Secondly, nothing is known about the tides in the ponds or, for that matter, in the outside waters adjacent to them. The nearest points recording tidal phenomena given in the

Coast and Geodetic Survey Tide Tables are Pt. Judith on the east and Watch Hill Point on the west and the time of mean high water differs by 50 minutes between these locations. Within the ponds, the tide range varies from zero to 2 feet depending on location as well as other undetermined factors and there is certainly variability in the time of tidal events and in their duration.

Despite regional differences and short term fluctuations it would seem that there has been a gradual rise in salinity at all stations during the 31 months of this study, though this event is most striking at stations 1 and 4. Perusal of the climatological data for the period shown in Table II would suggest that this may be simply the result of decreasing precipitation and increased solar radiation. In 1955 two major hurricanes

TABLE II. Pertinent monthly climatological data for 1955-1957

Month	Mean temperature, °F. Block Island			Monthly precipitation Block Island			Mean solar radiation g-cal/cm ² day Newport			Prevailing direction and average wind speed, MPH Providence		
	1955	1956	1957	1955	1956	1957	1955	1956	1957	1955	1956	1957
January.....	—	32.1	28.2	—	3.59	1.79	—	145	173	—	NW 12.4	NW 11.1
February.....	—	33.5	34.3	—	4.62	1.27	—	240	279	—	SW 11.1	SW 11.1
March.....	—	34.2	38.6	—	5.47	3.18	—	330	380	—	NE 12.1	NW 11.0
April.....	—	42.5	46.5	—	1.99	3.70	—	457	490	—	SW 12.3	SW 13.8
May.....	—	49.8	54.8	—	2.72	2.40	—	493	548	—	SW 13.1	SW 13.3
June.....	—	62.9	66.1	—	1.50	T	—	573	623	—	SW 10.3	8 12.9
July.....	—	62.1	69.3	—	4.35	1.84	—	521	521	—	SW 10.1	SW 12.1
August.....	72.0	69.0	67.7	6.34	1.63	5.62	399	448	452	SSW 9.8	SW 9.5	SW 10.1
September.....	63.5	61.9	65.1	3.07	1.86	1.58	411	378	365	NW 7.8	SW 10.1	SSW 10.9
October.....	56.5	54.8	54.6	8.74	2.30	2.42	243	312	249	SW 9.1	NW 8.8	NW 12.2
November.....	43.8	45.8	48.4	4.48	3.06	2.84	175	201	194	WSW 9.4	NW 11.0	SW 11.5
December.....	28.8	39.9	41.8	0.83	3.49	5.62	160	120	132	WNW 10.0	SW 10.6	SW 13.1
Mean.....	—	49.0	51.2	Total 37.49*	36.58	32.26	Mean 345**	352	366	Mean SW 10.0**	SW 11.0	SW 11.9

* Total for entire year.

** Mean for entire year.

"Connie" and "Diane" struck the northeastern United States bringing extremely heavy rains. In addition, another disturbance in October brought a 3-day downpour and extensive flooding in the middle Atlantic and New England states. Of the 37.49 inches of rain which fell in 1955, 22.63 inches fell during the first 4 months of this survey. In 1956 the yearly rainfall though only slightly less than 1955 was more evenly distributed and the ponds did not become markedly diluted at any time. The last year of the study, 1957, was characterized by rather low rainfall, especially in the winter and early summer. The mean temperature and mean solar radiation were also significantly higher than in the preceding year.

Although climatic factors were doubtless in large part responsible for the observed salinity increases, it is not certain that they were the only factors. During the winter of 1956-57 dredging was carried out at the breachway into Charlestown Pond and at the narrows between Charlestown and Green Hill. It is unfortunate that the dry year following these improvements obscured their effect on the ponds. Though the salinity at the remainder of the stations had started to fall by the end of January 1958, it remained high at station 4 in Green Hill Pond. (Since the ponds are partially or totally covered with ice in winter, the low values for surface salinity observed here and at other stations in January and February represents surface dilution by melt-water.) Only continuing observation can be expected to separate the effect of climatic changes from man-made influences.

Radiation and transparency

In Figure 3 the daily radiation received at Newport, Rhode Island is plotted for each sampling date, along with the surface and bottom extinction coefficients for stations 1, 2, 3 and 4. Although the percentage sunshine received at the surface of the Charlestown-Green Hill Pond system may differ somewhat from that received at Newport, the 2 localities are only about 19 miles apart and both are in proximity to the ocean so that the local climatic conditions should be similar.

Since the light extinction by these waters was measured with rather insensitive equipment and converted to the extinction coefficient *K* empirically, the values plotted in Fig. 3 cannot be expected to show more than gross differences between samples. Yet it is clear that the bottom water was almost invariably more turbid than the surface waters. There is little evidence for seasonal change in transparency, but rather periodic fluctuations, more probably related to wind direction and speed, were observed.

Surface extinction coefficients for stations 1, 2 and 3 were not appreciably different from each other and, at least part of the time, weekly changes were in the same direction for all stations. The surface waters in Green Hill Pond (station 4) were almost always more turbid than anywhere else in the Pond system. The mean value for *K* was higher than at the other stations. Dr. Robert McMaster, who has examined the bottom sediments in the ponds, observed a fine organic detritus in Green Hill which settled out very slowly.

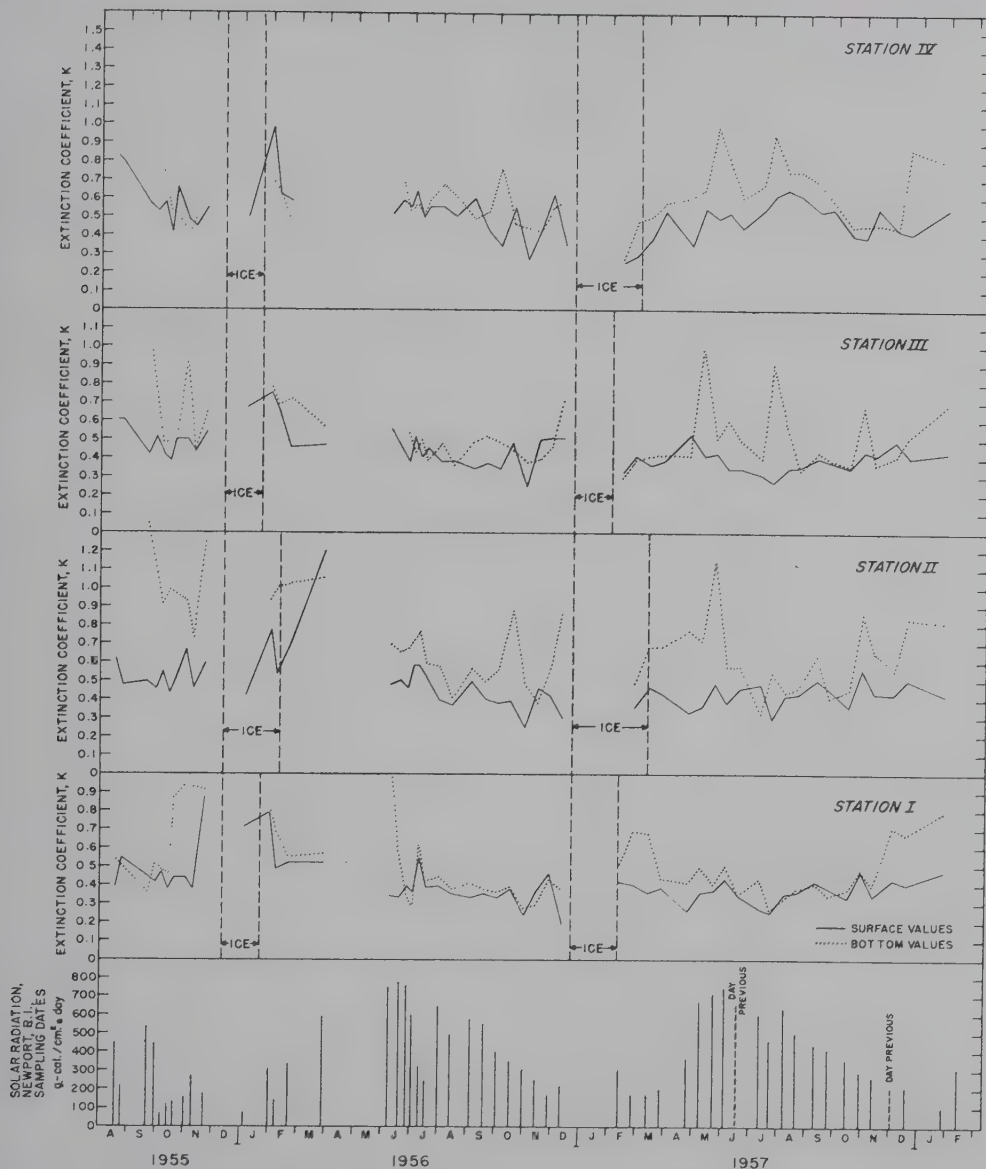


FIG. 3. Seasonal changes in the extinction coefficient K at stations 1-4 and the daily solar radiation recorded at Newport, R. I. on sampling dates.

To the casual observer the water in this pond appears to have a brownish color while that in Charlestown seems more nearly green.

In the bottom water, K was highest at station 2 and only slightly less at station 4. The high extinction values at station 2 were partially due to a sampling difficulty. Because of the luxuriant attached vegetation, often rising several feet from the floor at this station, it was a problem to get

a sample of water near the bottom without including pieces of algae and detritus associated with this flora. However, it is certain that this dense growth of plants must shade an appreciable portion of the water column, so that the extinction coefficient, no matter how accurately determined, would not give a true picture of the relative amount of radiation reaching all depths.

A detailed analysis of the factors affecting the

turbidity of the salt pond water is not warranted with the present data, but it would be interesting to have a general idea of the relative importance of the phytoplankton in the extinction of light in different parts of the pond system. Riley (1956) gave

$$K = 0.04 + 0.0088C + 0.54C^{2/3} \quad (2)$$

as the relationship between the extinction coefficient K and the amount of phytoplankton C , measured as μg of chlorophyll a per liter, based on a series of samples from offshore waters where suspended matter of non-planktonic origin should be minimal. In Long Island Sound this relationship invariably gave estimates for K appreciably less than those observed directly. Extinction coefficients calculated from (2) were generally lower than the observed values in the salt ponds as well, but the differences were usually not so great. When the mean differences were compared for stations 1-4, the stations were found to be significantly different, chlorophyll making the largest contribution to turbidity at station 2 and least at station 4. There was no significant dif-

ference in the contribution of chlorophyll to turbidity between surface and bottom measurements.

Distribution of phosphate and nitrate

The supply of inorganic phosphorus for biological production would seem to be low in the ponds in comparison with nearby coastal waters such as Block Island Sound or Long Island Sound. Values in excess of $1 \mu\text{g-at/liter}$ were very rare and, particularly in surface waters, the amount observed was usually less than 0.5 (Figure 4). Although only inorganic phosphates were run routinely, on 2 occasions total phosphates were also run. The comparison of these results (Table III) suggests that over 70% of the phosphorus was commonly in organic form, but nothing can be said at this time concerning its availability for primary production.

Phosphate showed little or no seasonal variation at any of the stations, but short term fluctuations were more pronounced and the amount typically greater at stations 2 and 3 (see Fig. 4). Because of the proximity of these stations to the

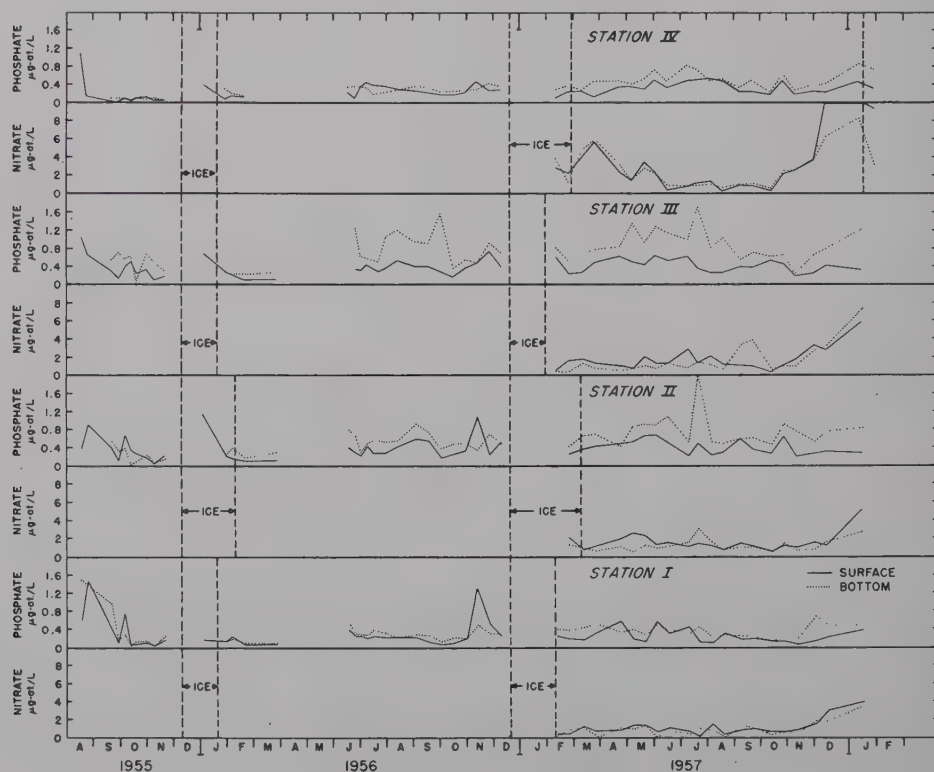


FIG. 4. Seasonal distribution of inorganic phosphate-phosphorus and nitrate-nitrogen at stations 1-4.

TABLE III. Comparison of total phosphorus and inorganic phosphorus

Date	Station	Total phosphate ($\mu\text{g-at/l}$)	Inorganic phosphate ($\mu\text{g-at/l}$)	Inorganic % of total
February 12, 1957.....	1 (surface)	1.15	0.25	21.7
	3 (surface)	1.26	0.59	46.8
	4 (surface)	0.89	0.18	20.2
	4 (bottom)	1.26	0.28	22.2
August 7, 1957.....	1 (surface)	0.97	0.11	11.3
	1 (bottom)	0.89	0.23	25.8
	2 (surface)	2.22	0.24	10.8
	2 (bottom)	2.22	0.54	24.3
	3 (surface)	1.15	0.24	20.9
	3 (bottom)	2.09	0.80	38.3
	4 (surface)	1.96	0.49	25.0
	4 (bottom)	1.78	0.47	26.4

breachway, the phosphate distribution here was probably more dependent on exchange with Block Island Sound than on biological utilization and regeneration within the pond itself. Phosphate was nearly always higher in bottom than in surface water. At stations 1 and 4, inorganic phosphate was usually lower than elsewhere, but the data indicate a slight increase during 1957, particularly in Green Hill Pond (station 4), which may reflect an increased exchange rate as a result of dredging operations during the winter of 1956-57. When phosphate measurements from all stations and depths were plotted against salinity, a positive linear correlation was obtained with correlation coefficient $r = 0.2715$ significant at $P < 0.01$.

The distribution of inorganic phosphate in the Charlestown-Green Hill system differed in some respects from Falmouth Great Pond, Massachusetts. In this environment Hulbert (1956) observed some seasonal increase in both inorganic and total phosphate, although the annual cycles were markedly different in different sections of the estuary. In addition, he found phosphate to increase from minimal values at mid-pond along a gradient shoreward to the fresh water source as well as seaward. A possible explanation for low phosphate in the runoff entering the Rhode Island ponds is given in a later section.

The seasonal and regional distribution of nitrate nitrogen was different in several respects from that observed for inorganic phosphate. Although nitrate levels were lower at station 1 than at stations 2 and 3, in contrast with phosphate, they were distinctly higher at station 4 than elsewhere in the pond system (Fig. 4). Furthermore, there was apparently a seasonal cycle of nitrate abundance in Green Hill with values in excess of $9 \mu\text{g-at/l}$ in winter decreasing to less than $1 \mu\text{g-at}$ during the summer months.

Nitrates apparently were increasing at all stations in December 1957 and January 1958. Perhaps a winter increase in this important nutrient would be expected for all stations and the absence of such an increase at stations 1, 2 and 3 during the winter of 1957 might be the exception. The rainfall for January and February of that year was only 44% of normal. Short term fluctuations in nitrate abundance also were characteristic of stations 2 and 3 but, more often than not, higher readings were observed in the surface waters than in bottom waters, in marked contrast with the vertical distribution of inorganic phosphate. The correlation between nitrate and salinity was negative and very significant ($r = -0.4207$; significant at $P < 0.001$).

Nitrate: phosphate ratios by atoms were usually very much lower than the concentration ratio of 15:1 characteristic of oceanic water (Table IV). Riley and Conover (1956) observed anomalous ratios similar to these in Long Island Sound and low ratios were also characteristic of the shelf waters south of Woods Hole (Ketchum, Vaccaro and Corwin, in press). However, winter nitrate: phosphate ratios in Green Hill Pond approached the expected values. The significance of nitrate and phosphate for production in the ponds will be discussed in greater detail in a later section.

TABLE IV. Monthly mean nitrate: phosphate ratios in surface and bottom waters, atoms of nitrogen to one atom of phosphorus

Sample	STATION 1		STATION 2		STATION 3		STATION 4	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
December 1956.....	1.6	1.4	1.5	1.2	1.4	0.9	14.6	11.9
January 1957.....	1.6	1.4	1.5	1.2	1.4	0.9	14.6	11.9
February.....	1.1	0.9	3.6	1.4	1.7	0.4	5.7	3.8
March.....	2.2	0.8	1.0	0.5	2.2	0.6	8.0	6.7
April.....	0.8	1.5	1.8	1.2	0.7	0.3	3.4	3.0
May.....	3.9	1.5	1.9	0.4	1.4	0.4	3.8	2.1
June.....	1.1	0.5	1.1	0.4	1.0	0.4	1.4	1.1
July.....	1.1	0.8	1.8	1.0	1.9	0.3	0.8	0.5
August.....	0.5	0.9	1.7	1.0	3.0	0.4	0.6	0.6
September.....	2.3	2.1	1.7	0.8	1.1	2.7	1.5	1.0
October.....	2.2	1.4	0.9	0.6	0.6	0.5	1.2	1.4
November.....	5.5	1.2	2.0	0.4	2.0	1.9	7.0	4.1
December.....	5.3	1.5	1.6	0.8	5.0	1.8	16.0	5.9
January 1958.....	4.5	3.0	7.9	1.4	8.6	2.7	10.6	4.5

Oxygen distribution

As might be expected in such shallow ponds, there was never any serious diminution of dissolved oxygen in the water column, but rather bottom waters were invariably highly super-saturated with oxygen during the summer months (Figure 5). Highest percentage saturation usual-

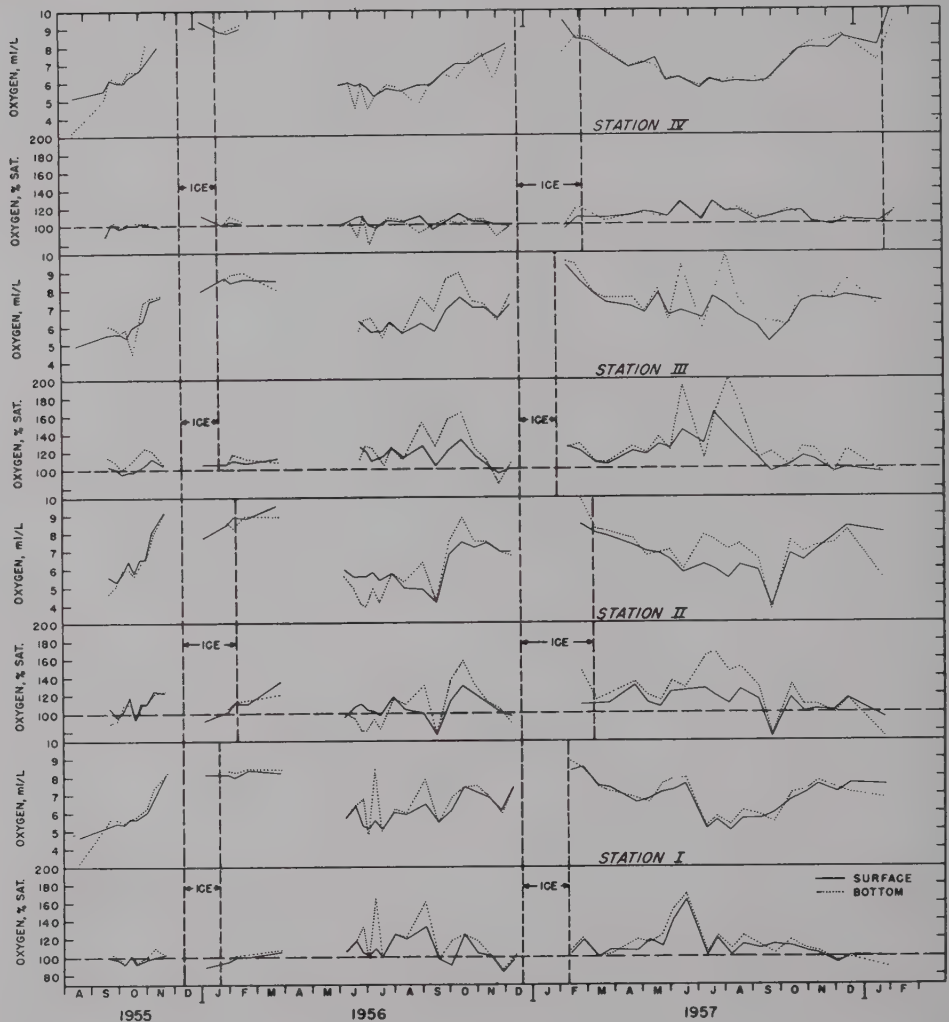


FIG. 5. Seasonal distribution of oxygen in ml/l and % saturation at stations 1-4.

ly occurred at stations 2 and 3; somewhat lower values commonly were found at station 1; and at station 4, the water was seldom highly supersaturated nor was there frequently a large difference in percentage saturation between surface and bottom waters. Almost certainly the distribution of oxygen in the ponds was related to the amount of attached vegetation. At stations 2 and 3 dense stands of the spermatophytes *Zostera marina* and *Ruppia maritima*, with associated "aufwuchs" of algae, were found often reaching the surface by the end of summer in 5 to 6 feet of water. A dense mat of algae and a few low

growing spermatophytes were characteristic of the western basin (station 1) while in Green Hill Pond (station 4) virtually no attached plants aside from some dwarfed *Zostera* near the opening of the "narrows" were encountered.

Distribution of chlorophyll

Chlorophyll fluctuations in the salt ponds are largely unpredictable and the seasonal cycles bear little resemblance to those commonly observed in temperate neritic waters (Figure 6). During the 2 years of the study there was no definite evidence to suggest a regular spring or winter

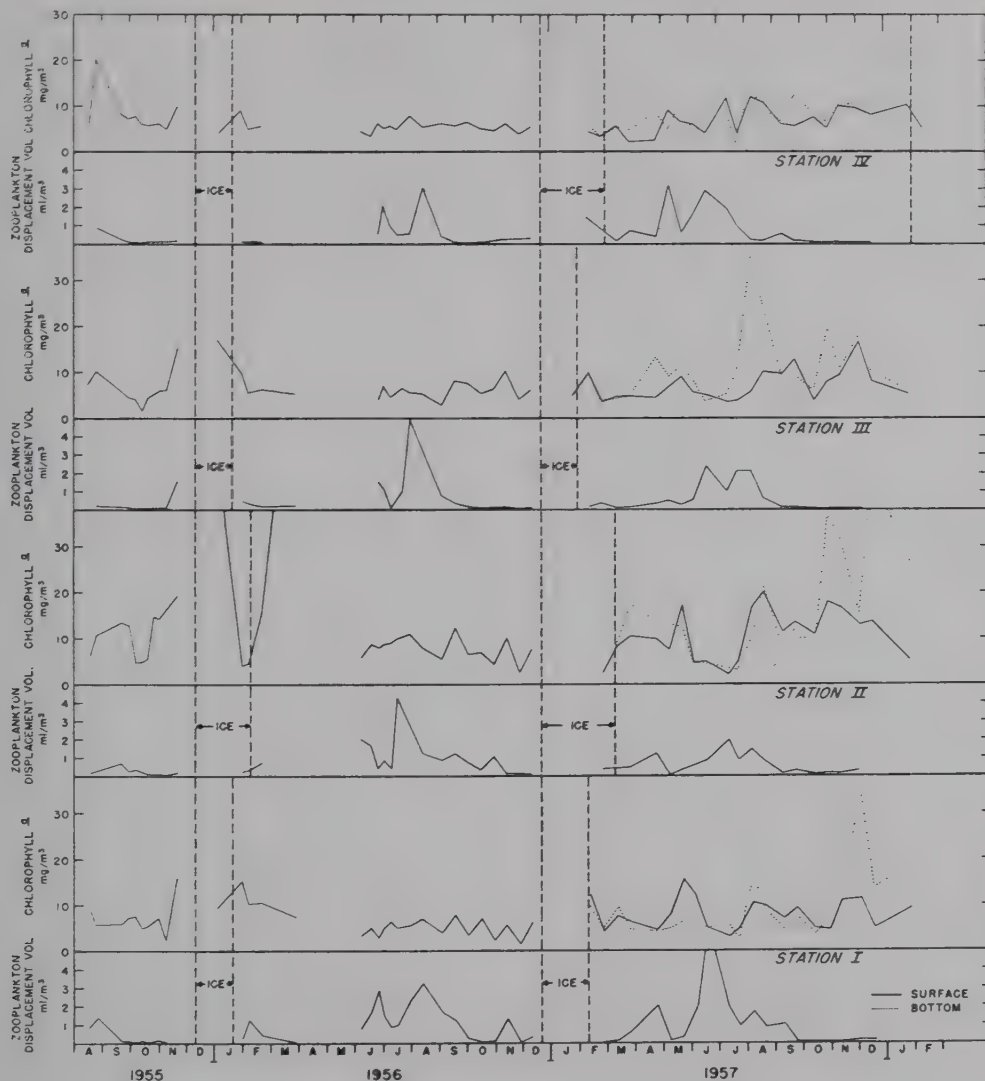


FIG. 6. Seasonal distribution of chlorophyll *a* and zooplankton displacement volumes at stations 1-4.

phytoplankton maximum, although very high chlorophyll values associated with brief "unialgal blooms" were observed on several occasions. Two such blooms occurred during the winter of 1956 and the dominant organism in each case was different. On January 4, 1956, when the ponds were largely ice covered, the heterokont *Olisthodiscus* sp. constituted over 99% of the sample, but on March 27 a species of *Gymnodinium* completely predominated. There was no evidence of mortality among other pond organisms during either of these blooms. During the late summer

and early fall of 1957 rather high chlorophyll values were found associated with a persistent bloom of the diatom *Chaetoceros curviretus* especially at stations 1 and 2. There were no comparable blooms in either 1955 or 1956 at the same season although a late summer growth of *Chaetoceros* has been observed in earlier years (H. P. Jeffries, personal communication). The variation in chlorophyll seems to follow the same sort of pattern of short term fluctuations observed for salinity and phosphate (see Figs. 2 and 4), and seasonal effects would seem to be of

secondary importance in the control of phytoplankton abundance compared with local conditions.

The distribution of chlorophyll *a* (Fig. 6) and percentage saturation of oxygen (Fig. 5) also showed relationships. Chlorophyll was highest in Fort Neck Pond and in the deep waters of the central basin. Oxygen was also highest in the deep water, though the water immediately adjacent to the breach, which had presumably only recently entered the pond, often was barely saturated. All estimates of the amount of bottom vegetation are based on visual observation. Chlorophyll measurements were undertaken as a quantitative measure of the standing crop of phytoplankton but in many portions of the pond the presence of the luxuriant attached flora interfered with the collection of representative samples of the interstitial water so that the bottom chlorophyll measurements often included bits of plant detritus and even fragments of living benthic algae. Possibly the bottom chlorophyll is a rough index of the abundance of attached flora and only surface chlorophylls give an estimate of the standing crop of phytoplankton. Still the abundance of chlorophyll and the percentage saturation of oxygen were tolerably correlated except near the breach and at the head of the northern cove, both locations which were being continuously diluted by water of lower oxygen content originating outside the pond system.

Distribution of zooplankton

In contrast with the phytoplankton, zooplankton abundance appeared to vary with season in a rather consistent fashion at all 4 stations (Fig. 6). Zooplankton volumes were low throughout the late fall, winter, and spring, but increased markedly in May or June and then decreased almost as abruptly in September. The curves shown in Fig. 6 have no apparent relation to the abundance of phytoplankton.

Several factors were in part responsible for this phenomenon. The longer life histories of plankton animals would tend to permit accumulation of organisms building up a large standing crop gradually over a period of time. Furthermore, in the salt ponds an appreciable portion of the zooplankton community was made up of the developmental stages of bottom invertebrates whose life cycles are seasonally controlled. At certain times of the year the salt ponds were invaded by coelenterates or ctenophores in large numbers. When captured in the plankton tows, these were counted and immediately discarded since they do not preserve well with formalin.

Hence, their biomass is not included in Fig. 6. There was invariably a sizeable pulse of the medusae *Aurelia aurita* and *Dactylometra quinquecirrha* during April and May, and many *Mnemiopsis leidyi* were found in September and October. In midsummer the ponds were completely free of these voracious carnivores and this was the season of largest standing crops for the other zooplankton.

Zooplankton volumes at the 4 major stations might be a useful index of production in the different portions of the pond, but there is one inconsistency which requires explanation. Zooplankton was abundant at station 2, the nutrient-rich, high chlorophyll waters of Fort Neck Pond (mean value, 0.64 ml/m³), and least in the relatively poor waters of Green Hill (mean, 0.48 ml/m³). However, highest zooplankton volumes were taken in the western basin (station 1, mean, 0.89 ml/m³) which is inconsistent with the other observations of the richness of the different sections of the environment. An explanation for this enigmatic distribution is suggested by qualitative examination of the composition of the samples. At stations 2 and 3, where the zooplankton volumes were relatively high, juvenile copepods and the larvae of benthic invertebrates invariably predominated. In the western basin and in Green Hill the fauna was predominantly copepod, and all stages including a large adult population were found. The exchange rates for the various portions of the pond leave little doubt that the water in the central portions of the pond system must be renewed much more rapidly than the water in the relatively isolated basins on either side. In the central regions, a high rate of reproduction was characteristic of the zooplankton populations, but few individuals remained in the area long enough to reach adulthood. In the isolated basins, although the actual production rate for the zooplankton may have been lower, the relative stability of the water mass permitted greater accumulation of the end product.

REGIONAL DIFFERENCES IN PRODUCTIVITY

The distributions of chlorophyll, oxygen, and perhaps zooplankton suggest that highest levels of productivity are found in the regions coming under the influence of the breach. Macroscopic flora was also most luxuriant in this region. Preliminary investigation of the abundance of benthic organisms and particularly the distribution of *Crassostrea virginica*, the principal economic species in the ponds, supports the hypothesis that the central regions of the system are the most productive.

A number of light bottle-dark bottle experiments were run at the different stations at different seasons. Because this method at best measures only the phytoplankton production, in these ponds where benthic plants are important, the results of these experiments give only a qualitative picture of productive capacity in different regions. Mean gross photosynthesis was highest at station 2, next highest at station 3, while stations 4 and 1 were substantially lower than either of the more productive stations.

EVALUATION OF THE FACTORS CONTROLLING PRODUCTION

Although temperature and salinity are known to have qualitative effects on the populations in any given body of water, neither would seem to be a critical factor in the control of total productivity. In a similar estuarine system, Ryther (1954) found that certain "small forms" formed dense growth in waters of 1 ‰ salinity where there was adequate fertilization from the waste of duck farms. In the same area, he found representative phytoplankton which maintained a high division rate over a range of temperature from 5 to 30° C in culture experiments. Therefore it seems highly probable that other factors play the more important role in the maintenance of production in the salt ponds.

Light and turbidity

It has been postulated by Poole and Atkins (1929) that the extinction of surface radiation with depth followed the exponential relationship

$$I_d = I_0 e^{-kd} \quad (3)$$

in which k is the extinction coefficient, I_0 the surface intensity and I_d the intensity at depth d . Using the bottom extinction coefficients from Fig. 3 and the monthly mean radiation data supplied by the Eppley Laboratories at Newport, it can be shown that the minimum daily average radiation, except during periods of ice cover, penetrating to the bottom at any station sampled in the ponds was about 30 gcal/cm² day at station 2 in Fort Neck Pond during December 1956. Edmondson (1956) stated that about 50% of the radiation measured by the pyrhelimeter was in the visible range and might be used in photosynthesis. Thus 15 gcal could be taken as a lower limit for energy available for primary production in the ponds.

Rabinowitch (1951) gives 0.0014 gcal/cm² min or 2.0160 gcal/cm² day as the compensation intensity for *Chlorella*. With the marine diatom *Coscinodiscus excentricus*, Jenkin (1938) observed a compensation intensity equivalent to

3.125 gcal/cm² day. Although nothing can be said about the amount of radiation needed by the complex plant populations of the salt ponds to maintain a balance of photosynthesis over respiration, the minimum value of 15 gcal received allows a considerable margin for error before insufficient light alone could bring about even temporary cessation of primary production in the ponds. The lack of a marked seasonal accumulation of nutrients (see Fig. 4) would tend to confirm the hypothesis that primary production continues at a relatively high rate throughout the year.

To residents along the shores of the ponds the preceding arguments might seem of doubtful validity since it is well known that in October or November every year a large portion of the standing crop of plants becomes detached from the bottom and is deposited on shore-line property. However, evidence strongly suggests that this phenomenon results from mechanical destruction of the community rather than physiological quiescence followed by loss of chlorophyll-bearing structures as in deciduous land plants.

As mentioned earlier, the spermatophytes, which are probably the most important units in the attached plant community, grow to a height of 4-6 ft during the periods of relatively small turbulence in summer carrying with them a dense growth of epiphytic algae. As this community grows upward it becomes more and more unstable mechanically so that by the end of September a good southwest gale supplies more than enough turbulent energy to tear the plants loose from their rhizomes. The mechanical and bacterial degeneration of this material returns a significant portion of the stored nutrients and organic matter to the pond for use in further production.

Although diminished incident radiation and high turbidity did not appear to limit production in the ponds, they certainly affected the production rate from day to day. During the summer and early fall of 1956, on several occasions, replicate water samples from all stations were used for *in situ* photosynthesis experiments at each station. The amount of oxygen produced was then compared as a randomized block experiment using the analysis of variance. Not only was the amount of photosynthesis significantly different for the water from the different stations, but also the locations of the sets of experiments had significant effects on the photosynthesis. The amount of photosynthesis was not perfectly correlated with the amount of radiation received at each location, but it is possible that in midsummer the radiation levels were too high for op-

timum production where the turbidity was low at the 1 meter depth used. In any case, smallest amounts of photosynthesis occurred where the extinction coefficient was highest.

Nutrients

Phosphate and nitrate were significantly correlated with salinity but in the case of phosphate the correlation was positive while with nitrate the correlation was negative. This interesting inverse distribution of these important nutrients presents a special problem in the evaluation of the relative importance of each in the biological cycles of the ponds. Chlorophyll was also found to have a significant positive correlation with salinity which might suggest that phosphate was the nutrient limiting primary production. However, both substances are known to be necessary to plant growth, and both are, at times, low in the pond systems. Therefore, multiple and partial correlation techniques were used to evaluate the role of phosphate and nitrate together and separately in the economy of the pond.

The multiple regression equation

$C = 0.184S + 5.570P + 0.184N + 1.983$, (4)
where C is chlorophyll a in $\mu\text{g/l}$, S is salinity in ‰, P is inorganic phosphate in $\mu\text{g-at/l}$ and N nitrate also in $\mu\text{g-at/l}$ has a multiple correlation coefficient $R_{\text{SNP}} = 0.280$ significant at better than 1%. This equation might be used to predict the standing crop of phytoplankton in terms of $\mu\text{g/l}$ of chlorophyll a from salinity and nutrient data alone. The expression

$$s_c = \frac{(1 - R_{\text{SNP}}^2)Sc^2}{n} \quad (5)$$

where s_c is the standard error of estimate for chlorophyll in $\mu\text{g/l}$, Sc^2 is the sum of the squared deviations of the individual observations from the mean chlorophyll a estimate, R_{SNP} is the multiple correlation coefficient for (4) and n is the degrees of freedom, can be used to predict the error in such estimates (modified from Snedecor 1946). The standard error of estimates $s_c = 7.36 \mu\text{g}$ chlorophyll a /liter leads to a coefficient of variation of about 74% which would seem to make the use of expression (4) to predict chlorophyll values of little practical application. Although, bottom chlorophyll estimates are probably not a good measure of the standing crop of phytoplankton because of contamination of the samples by chlorophyll of benthic origin, the chlorophyll estimates would seem to be the best index of the standing crop of all primary producers presently available for the ponds. If only surface values are used in the regression analyses,

no significant correlations are found except between salinity and nitrate (negative).

The relative importance of the different variables contributing to the multiple regression equation (4) may be more precisely evaluated by use of partial correlation coefficients. With this technique the correlation between any 2 sets of variables may be studied independent of variability in one or more of the additional sets of measurements. Thus the partial correlation coefficient $r_{\text{CP.S}}$ measures the degree of correlation of chlorophyll and phosphate when salinity is held at a constant value.

Pertinent partial correlation coefficients for the relationship between salinity, phosphate, nitrate and chlorophyll are given in Table V. The coefficients No. 1-4 re-emphasize the strong correlation between salinity and both nitrate and phosphate. Furthermore, these correlations are independent of other variables. Salinity and chlorophyll are correlated independent of nitrate (No. 6) but phosphate apparently is necessary for the correlation as shown by No. 5. In other words, the distribution of phosphate would seem to be important to the distribution of chlorophyll while nitrate does not matter very much. Numbers 7 and 8 show even more definitely that nitrate and chlorophyll bear no direct relationship, while Nos. 9 and 10 reiterate that phosphate and chlorophyll are strongly correlated regardless of salinity and nitrate concentrations. In No. 11 the correlation of salinity and chlorophyll is tested independent of both nitrate and phosphate. Since the correlation is not significant, the important position of phosphate in the economy of the ponds is more firmly established since the independent position of nitrate shown in No. 6 is statistically less important than the dependence on phosphate for the correlation between salinity and chlorophyll.

This analysis does not prove that phosphate was the limiting factor for chlorophyll abundance, for it is perfectly possible that some unmeasured variable correlated with phosphate but not nitrate or salinity could be responsible for the result obtained. Nor do the results indicate that nitrate is unnecessary but only that the supply was adequate.

Regression analysis for each of the individual stations gave significant correlations between chlorophyll and phosphate for stations 3 and 4 but, interestingly, no significant correlations with chlorophyll were found for any of the 3 dependent variables tested for station 2. Only at station 1 was chlorophyll significantly and positively correlated with nitrate ($P < 0.02$), but

TABLE V. Partial correlation coefficients for salinity, inorganic phosphate, nitrate and chlorophyll data for all stations and 2 depths

Partial correlation coefficient	Value	Level of significance	No.
r_{SP-N}	0.3350	<0.01	1
r_{SP-C}	0.2382	<0.01	2
r_{SN-P}	-0.4595	<0.01	3
r_{SN-C}	-0.4279	<0.01	4
r_{SC-P}	0.1159	>0.05	5
r_{SC-N}	0.1960	0.01	6
r_{NC-P}	-0.0170	>0.05	7
r_{NC-S}	0.0861	>0.05	8
r_{PC-N}	0.2541	<0.01	9
r_{PC-S}	0.2171	<0.01	10
r_{SC-NP}	0.1305	>0.05	11

there was no correlation with phosphate. Partial correlation coefficients were computed for the individual stations, but they offered no new information.

Exchange and runoff in the maintenance of nutrients. In a pond system of this sort the influence of runoff and exchange are considerable. The exchange rate between Charlestown Pond and Block Island Sound and between Green Hill Pond and Charlestown was measured directly only once during the two and a half years of the program, and it seems very unlikely that the data acquired can be typical. On this occasion, December 1, 1955, the ebb tide at the breachway was of about 9 hours' duration and at the narrows between the ponds was over 10 hours.

During the tidal cycle studied, about 1,300,000 m³ or 19% of the volume of Charlestown Pond (about 15% of the entire system) was lost through the breach but only 650,000 m³ or about 50% of the amount lost was returned. During the same tidal cycle 18,000 m³ of fresh water entered Charlestown Pond and a net gain of 19,900 m³ entered from Green Hill leaving a substantial net loss. At the narrows about 12% of the volume of Green Hill was lost to Charlestown and less than 1% was returned during this tidal cycle from all sources. Even assuming that the tidal cycle observed was highly atypical, the daily exchange between Block Island Sound and the salt ponds must be considerable.

Slightly better data are available on stream runoff and they are summarized in Table VI.

Pond volumes shown in this table and used for the calculations in the previous paragraph were determined by planimetry of the bathymetric contours. The volume of the breachway system was determined from the cross-sectional area between the stone breakwaters at its entrance and the average length of the tidal river connecting with the ponds.

TABLE VI. Area, volume and fresh water runoff

	Area acres	Total volume m ³	Fresh water entering/ day * m ³	% Total volume
Breachway.....	—	32,500	—	—
Charlestown Pond.	1561	6,886,500	21,000	0.30
Green Hill Pond...	420	1,819,800	23,000	1.26
Entire system.....	1981	8,738,800	44,000	0.50

* Average of 4 sets of observations at different times of the year.

It is clear that stream runoff did not generally amount to more than 1% of the total pond system volume in 24 hours. Of the fresh water entering from streams over half entered Green Hill, the smaller basin, which was appreciably more dilute than the rest of the system.

The area of the drainage basin of the ponds was estimated to be about 7600 acres. Using the rainfall data from Table II, it can be calculated that roughly 76,000 m³ of water on the average are distributed over this drainage basin each day. Thus an excess of 32,000 m³ presumably must be lost to the atmosphere by evaporation and transpiration or enter the ponds as groundwater.

Since the single direct measurement of exchange was entirely inadequate to estimate the rates for Green Hill and Charlestown Ponds, an indirect method was employed to obtain a rough estimate using the average salinities and the amount of runoff. The fraction of fresh water F in a segment of an estuary can be determined from the ratio of the observed salinity in the segment S_1 and the salinity of the more saline water mixing with it, S_2 , as

$$F = (1 - \frac{S_1}{S_2}) \quad (6)$$

Then the total accumulation of fresh water will be equal to F times the volume of the segment. According to Ketchum (1951) the exchange ratio r_n per unit of time can be calculated from the expression

$$r_n = \frac{R}{Q_n} \quad (7)$$

TABLE VII. Calculation of exchange rates for different regions of the Charlestown-Green Hill Pond system

	Salinity of mixing water	Mean salinity	Total volume	Accumulated fresh water m ³ Q _n	River water entering/day m ³ R	Exchange rate %/day r _n	Net volume of water lost from each seg- ment in a seaward direction
Fort Neck Pond referred to Block Island Sound	30.8	27.4	1,095,000	120,800	21,000	17.4	190,500
	31.6	27.4	—	145,600*	—	—	—
Green Hill Pond referred to Block Island Sound	29.0	16.9	1,819,800	759,200	23,000	3.0	54,600
	31.6	16.9	—	846,200*	—	—	—
Western basin referred to Block Island Sound	28.4	27.4	3,908,500	137,600	—	—	—
	31.6	27.4	—	519,800*	—	—	—
Central basin and Breachway	31.6	29.9	1,915,500	103,000*	44,000	42.7	817,900
Total.....	—	—	8,738,800	1,614,600	—	—	—
Entire Pond.....	31.6	25.74	8,738,800	1,616,700	—	9.4**	—

* Accumulated fresh water volumes used to compute total accumulated fresh water.

** Calculated from total volume of water lost from central basin to Block Island Sound referred to the volume of the entire pond system.

where R is the volume of runoff per unit of time and Q_n is the volume of fresh water accumulated in the n^{th} segment.

Table VII summarizes the procedure used to make the exchange calculations for the salt ponds. The pond was divided into the 4 principal basins or regions discussed at length previously. The accumulated fresh water Q_n was computed for each section. For the sections receiving measurable stream runoff, r_n was also calculated. The western basin received no measurable stream flow so that no exchange ratio could be computed. Yet this basin has accumulated an appreciable amount of fresh water presumably from seepage and springs along its shore. Because the amount of ground water entering the ponds is unknown, all exchange estimates must be considered minimal.

An additional word of explanation should be made concerning the values of accumulated fresh water marked with the asterisk. These values represent total fresh water accumulated by each segment with reference to the outside mixing sea water and their sum should equal the total accumulation determined from the weighted mean salinity as shown in the last row of the table. The discrepancy between the 2 values is almost certainly the result of rounding off during the calculations.

The calculation of exchange for the whole pond cannot be made with the weighted mean salinity, however, as water of this salinity is never found near the breachway and thus is never exchanged directly. The water exchanged by the whole

pond is the same as that exchanged by the central basin with Block Island Sound. The net volume lost from the central basin shown in column 7 was divided by the volume of the whole pond to give the exchange ratio for the entire pond system.

It is well known that a two-layered transport system operating in a typical estuary usually results in frequent enrichment and the maintenance of high concentrations of nutrients. The effectiveness of this mechanism even in such a shallow embayment as the Charlestown-Green Hill system is shown in Figure 7. Very little of the nutrients entering the pond on any flood tide would seem to be lost on the ensuing ebb. Within 30-45 minutes from the time the tide turns from flood to ebb, low salinity and low phosphate water characteristic of the ponds was observed at the breach. Apparently the more dense, nutrient-rich water from offshore slid beneath the less dense pond water displacing it upward, so that only the surface layers flowed out over the shallow sill on the ebb tide. Clearly the presence of such a sill increases the tendency for nutrient concentration by a 2-layered transport system and may explain in part the apparently high productivity of coastal ponds of the Charlestown-Green Hill variety.

Assuming that the exchange rates and runoff data presented in Tables VI and VII are approximately correct, it is possible to estimate the mean contribution of nutrients to the pond system through each mechanism as shown in Table VIII. The calculations were made in the following manner. Taking the exchange ratio for Fort Neck

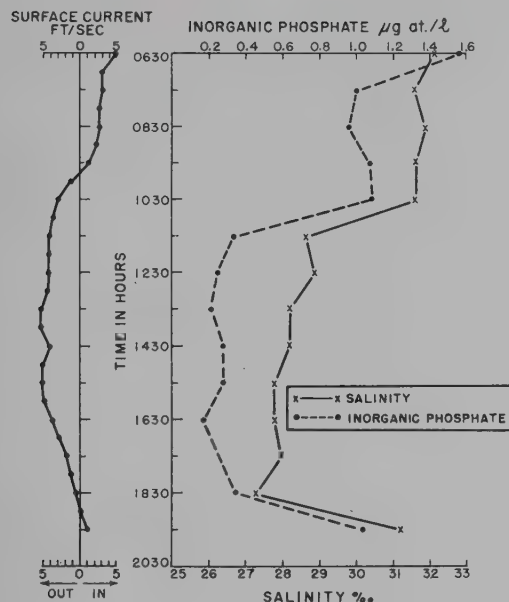


FIG. 7. Distribution of salinity and phosphate with respect to time, and direction and speed of tidal current at the breachway, December 1, 1955.

Pond (Table VII), it is clear that 0.174 of the total volume will be lost in a seaward direction each day and this must be replaced by fresh water from land and by salt water mixed in from the immediately seaward section. Since the fraction of the exchange water replaced by runoff is known (Table VI), the fraction contributed from the seaward direction can be computed by difference. The mean nutrient concentration in the surface water of the section times the exchange fraction gives the loss per unit volume from Fort Neck. Nutrient levels in the runoff and in the deep mixing water were multiplied by the appropriate fractions to compute the gain in nutrients by the exchange process. Calculations for Green Hill were made in the same way, except that all water exchanged is surface water because of the "narrows" sill and surface nutrient levels were used. In the case of the central basin a slight complexity is added in that nutrients are lost in a landward as well as a seaward direction through mixing into Fort Neck and Green Hill Ponds.

From Table VIII it is readily seen that a considerable net gain of both phosphate and nitrate is contributed to the pond system from Block Island Sound. A major portion of this enrichment does not seem to get beyond the central basin, the contribution to Green Hill Pond being particularly small. Because runoff is a relatively

small fraction of the pond volume, the nutrient contribution would seem to be relatively insignificant. This statement is probably true in the case of phosphate, which is always low in the runoff, but in the case of nitrate the greater accumulation of fresh water in Green Hill Pond must account for the larger standing crop observed. Over 3 times as much nitrate is acquired from runoff as from Charlestown Pond by exchange.

The drainage basin of the ponds is largely agricultural land or colonies of summer cottages. Virtually no indication of industrial or domestic pollution was detected. The higher nitrate concentrations in the streams and ground water may be derived from heavily fertilized potato fields in the area but, according to Dr. Robert Bell (personal communication), the acid local soil binds phosphate so tightly that even with heavy applications of lime, little would be lost through leaching.

AN ESTIMATE OF COMMUNITY PRODUCTION FROM PHOSPHATE

Rates of change of phosphate have been used by several authors to compute primary production. Some of the arguments for and against the use of phosphate for this purpose are discussed by Steele (1956). However, in these ponds there is no seasonal accumulation of inorganic phosphate nor seasonal change in the vertical distribution so that rates of change except over very short time intervals are virtually impossible to determine directly.

In shallow ponds where there is sufficient light to permit photosynthesis at all depths in all seasons phosphate can be used to estimate "net" production in another sense. The present work suggests that over a period of a year or more the pond system is in a steady state with respect to phosphorus. If the ponds were a closed system, this would imply that one atom of phosphorus would be regenerated for every atom used, so that no net increase in the standing crop would be possible and only such net production would occur as was necessary to maintain the *status quo* at the next trophic level. Salt ponds are not a closed system and they have the advantage that the rates of nutrient enrichment can be simply if crudely calculated. This "excess phosphate" must be largely incorporated into plant tissue initially. Since only inorganic phosphate was estimated routinely, it is possible that the net gain in inorganic phosphate shown in Table VIII could be balanced by a net loss of organic phosphate, but it is immaterial to the argument whether organic matter is accumulated in the

TABLE VIII. Balance sheet for phosphate and nitrate gained and lost through runoff and exchange

PHOSPHATE						
	Mean phosphate standing crop mg-at/m ²	Gain phosphate mg-at/m ² day		Loss phosphate mg-at/m ² day		Net gain or loss mg-at/m ² day
		from landward section	from seaward section	to landward section	to seaward section	
Fort Neck Pond.....	0.465	0.0100	0.1138	—	0.0682	+0.0556
Green Hill Pond.....	0.277	0.0027	0.0065	—	0.0078	+0.0014
Western Basin.....	0.309	—	—	—	—	—
Central Basin and Breachway.....	0.552	0.0463	0.4040	0.0711	0.1627	+0.2165
Entire Pond.....	0.487	0.0018	0.0890	—	0.0358	+0.0550

NITRATE						
	Mean nitrate standing crop mg-at/m ²	Gain nitrate mg-at/m ² day		Loss nitrate mg-at/m ² day		Net gain or loss mg-at/m ² day
		from landward section	from seaward section	to landward section	to seaward section	
Fort Neck Pond.....	1.43	0.045	0.240	—	0.275	+0.010
Green Hill Pond.....	3.04	0.087	0.028	—	0.097	+0.018
Western Basin.....	1.06	—	—	—	—	—
Central Basin and Breachway.....	1.58	0.250	1.018	0.164	0.692	+0.412
Entire Pond.....	1.80	0.025	0.224	—	0.152	+0.097

environment or transported elsewhere. If a steady state exists, the fact remains that only in an open system can there be an excess of organic matter produced in the long run over the immediate community needs. Thus the "net" production discussed here is analogous to but not synonymous with the excess of assimilation over respiration at a single trophic level.

In order to determine the magnitude of this net community production per m² it is only necessary to multiply the net gain in phosphate in mg by the carbon-phosphate ratio by weight (41:1) and correct for depth of the water column as shown in Table IX. Green Hill Pond and probably the western basin accumulate little or no organic matter produced *in situ*, although they probably acquire some produced elsewhere.³ Both Fort Neck Pond and the central basin fix carbon in excess of the over-all pond average which is in agreement with observations mentioned earlier. For the central basin this net community production is in excess of 135 g carbon/m² year.

³ Mention has been made earlier of a fine organic detritus in Green Hill Pond. It is believed that this organic matter represents past production *in situ* but there is little evidence that present production is adding significantly to it. As recently as 1948 or 1949 Green Hill supported large populations of *Chara* sp. and other pondweeds (Dr. R. D. Wood, personal communication). These have completely disappeared, presumably as a result of salinity increases since the breachway enlargement in 1952.

This is not a very large amount compared with coral reefs studied by Sargent and Austin (1954), Odum and Odum (1955), and Kohn and Helfrich (1957) or for a marine turtle grass bed (Odum 1956) or a large spring (Odum 1957). The important point to be made, however, is that the 2-layered circulation system involving a sill at the mouth of the estuary almost certainly retains a high percentage of the organic material produced there, while in the case of coral reefs and other types of flowing water communities a significant amount of the organic matter in excess of community needs becomes transported elsewhere.

TABLE IX. Net community production for the Charlestown-Green Hill Pond system

	Net gain in phosphate mg/m ² day	Mean depth meters	Carbon fixed mg/m ² day
Fort Neck Pond..	1.72	1.42	100
Green Hill Pond..	0.04	1.07	2
Central basin.....	6.71	1.36	374
Entire pond system	1.70	1.09	76

Clearly the salt pond environment is not a climax community and it is strongly autotrophic according to the classification of Odum (1956). Without a better measure of how fast the cycles within the pond are completed it is not possible

to compare production in the salt ponds with other environments quantitatively.⁴ However, it is probably safe to state that most of the highly productive marine communities, at least those which are highly productive of economic species, are non-climax and autotrophic. Thus one of the chief problems in the management of ponds such as these for commercial ends will be to prolong the sub-climax condition as long as possible.

DISCUSSION

The preceding arguments have demonstrated the desirability for exchange between the ponds and the offshore waters. It seems clear that a considerable portion of the essential nutrients for continued production are introduced by this process and the regions nearest the breach are definitely more productive than more remote regions.

Perhaps less clear but equally important is the role of fresh water in the maintenance of high productivity, especially of economic species. Obviously, land drainage does contribute a smaller but probably significant amount of nutrients, particularly nitrate, to this pond system. In other areas the nutrient load of fresh waters entering an estuary may be appreciably higher, although this does not necessarily ensure a high productivity of useful forms. Before the duck farms became well established in the drainage basin of Moriches Bay and Great South Bay, Long Island, these bodies of water supported a substantial oyster industry. The increased nutrient supply from these farms very probably has increased the primary production of "small forms" in the estuary, but the oysters all but disappeared (Ryther 1954).

Land drainage is important for at least 2 additional reasons. In the first place, a head of fresh water in any estuary causes a net seaward transport which helps to maintain an opening through obstructing bay-mouth bars against the forces of wind and tide operating to close it. Secondly, dilution provides waters of different densities in the estuary thus setting up a 2-layered system with less dense water flowing seaward at the surface and dense water from offshore flowing in along the bottom. The interaction of the 2 components moving in opposite directions creates an "eddy" which can concentrate nutrients and organisms. The importance of a sill to this process in even a shallow estuary has al-

ready been pointed out. Thus ponds of the sort described here are a kind of natural "culture basin" provided with a frequently renewed culture medium but also provided with an entrapment mechanism to prevent excessive loss of the products of the culturing process.

Despite the obvious desirability of appreciable exchange between a salt pond and the offshore waters, there is considerable danger in altering a natural breachway or enlarging existing ones. It has been emphasized that these ponds are transient and that increasing tidal exchange tends to speed up the natural processes which eventually will eliminate the present form of the environment. It should also be pointed out that increasing the dimensions of the breach will only increase the exchange temporarily and, unless almost continuous dredging is carried out in the breachway and in the ponds, dynamic forces will tend to close the mouth and silt up the channel until a natural, though usually temporary equilibrium is re-established. This equilibrium will most likely be a function of the tidal range, volume of the ponds and fresh water head, all of which are usually beyond human control.

There is a feeling among some local residents that enlarging the present breach or adding an additional breachway into the western basin would tend to eliminate the dense macroscopic attached flora which is a nuisance to shoreline property owners. The evidence tends to contradict this hypothesis. Comparison of the present distribution of attached aquatics with the brief description in Wright, Cheadle and Palmatier (1949) suggests considerable increase in the range and abundance of both *Ruppia maritima* and *Zostera marina* since the breachway enlargement in 1952. When the exchange rate in an environment is greater than some desired optimum, it is very probable that the pelagic organisms are dispersed before a sizeable standing crop can develop regardless of the supply of available nutrients. Under these conditions, only the attached aquatics can satisfactorily utilize the increased enrichment. A stage in some ways comparable to advanced eutrophication in lakes then may develop.

Evidence is strong that the critical exchange rate has already been exceeded in Charlestown Pond, presumably through dredging operations in 1952 and 1956. In brackish embayments, the chief marine crops feed principally on phytoplankton and if the standing crop of phytoplankton is depleted the growth rates of the shellfish will probably be affected. In addition to swinging the balance of primary production from the desirable phytoplankton to the less desirable attached

⁴ Gross production based on light and dark bottle experiments, which presumably measured only photosynthesis by the phytoplankton, amounted to 24.2 g carbon/m² year. Though no quantitative data are available, the phytoplankton probably contributes only a small fraction to the total productivity of ponds such as these.

forms, the excessive exchange probably affects the growth and distribution of oysters in other ways. Greater exchange increases the probability that the pelagic larvae of the oyster will be swept from the ponds or to some other unfavorable location before they are ready to set. Furthermore, the greater exchange also means greater tidal scouring and hence greater sediment transport within the ponds. Suspended matter and the pelagic oyster larvae both will tend to settle out in the same areas such as the sheltered coves along the edge of the moraine. It is well known that excessive silt deposition will depress growth rates or even kill oysters. Thus, in Charlestown Pond it is not surprising that formerly rich oyster beds associated with glacier deposits in the central basin are now quite barren and, where oysters still are found in the sheltered coves of Fort Neck Pond, their growth rates are depressed.

In order to make maximum use of the potential for useful production in ponds such as these, an optimum ratio of flushing and exchange must be determined. Quite possibly the optimum breachway would be near or only slightly larger than that which would remain when dynamic forces had returned the ponds to the temporary equilibrium condition mentioned earlier. This does not necessarily mean that breachway improvements are useless. Rather they should be developed with a view to making the temporary equilibrium conditions more permanent. Dams with tide gates to control the tidal exchange and flushing rates regardless of variation in rainfall and tide range might be inserted in present breachways. Such gates might also be designed to open when necessary to permit small boat traffic and furnish access for migratory forms. Also groins might be employed to regulate the movement of sand along the barrier beach in the vicinity of the breach.

Just as there is an optimum breachway condition for any pond system, there is almost certainly an optimum size for the pond itself which is chiefly a function of the drainage basin and amount of fresh water received. The present survey suggests that the elimination of the western basin and Green Hill Pond would have only slight effect on the total annual production of marine crops from the pond system. Since the amount of fresh water entering the pond is frequently beyond human control, as is significantly altering the size of a pond, all ponds cannot be made equally productive. However, in the case of Charlestown-Green Hill, altering the size of the drainage basin and the size of the pond itself is technically feasible. That the drainage basin could be altered

was recognized as early as 1734. Northwest of Fort Neck Pond the moraine which separates the Pawcatuck and Charlestown-Green Hill watersheds is interrupted by Indian Cedar Swamp, a marshy wasteland which drains both north and south. At this point the divide separating the watersheds is not over 10 feet and could easily be breached. A controlled supply of water could almost certainly be removed from the Pawcatuck without seriously affecting conditions on the lower river.

The effects of this alteration on the pond system cannot be determined precisely at this time but almost certainly the problem of breachway maintenance would be diminished. If a portion of this fresh water could be diverted into the western basin of Charlestown, a significant increase in the productivity of that region would be anticipated.

A 2nd major alteration in the present pond system could be carried out at considerably less cost. It is highly probable that the exchange rate for Green Hill is currently less than would be necessary for optimum productivity. A small breachway could easily be cut through the barrier beach into this pond. Tidal gates which can be regulated to control exchange should be installed in this breach and also at the narrows between Charlestown and Green Hill. Several years of experimentation would be necessary to determine the critical exchange rate for this environment, but because it is a smaller, more homogeneous basin, problems of regulation could be more readily solved than in the larger pond.

SUMMARY

A survey of Charlestown Pond and Green Hill Pond, Rhode Island was carried out from August 1955 to February 1958. Observations of temperature, salinity, oxygen, inorganic phosphate and nitrate, chlorophyll *a* and zooplankton displacement volume were made at several stations about twice a month. The ponds are shallow, not over 10 feet in depth, but cover an area of 1980 acres. It is concluded that the volume and probably the area have been appreciably reduced in the past 300 years as a result of organic production *in situ* and the wave and tidal forces operating against shifting sand deposits. Despite the shallow water column some salinity stratification is maintained and a 2-layered transport system serves to enrich the regions proximal to the breachway. There were no marked seasonal cycles for inorganic phosphate or nitrate and the distribution of these substances seems more dependent on physical than biological factors. It was shown by means of

regression and correlation analysis that phosphate, derived principally from exchange with offshore waters, was limiting to production over most of the pond system, but in the western basin of Charlestown Pond which receives virtually no land runoff nitrate may be the limiting nutrient. The waters, especially the bottom waters, were generally super-saturated with oxygen and this is believed to result from high rates of photosynthesis by the dense growth of attached spermatophytes and associated algae. It is believed that most primary production in the ponds is associated with this attached vegetation. Phytoplankton chlorophyll *a* values were not particularly high, but the distribution over the pond system was a good index of the relative productive capacity of the different regions. Because of the shallow water sufficient light for photosynthesis was usually available throughout the year, and this is doubtless in part responsible for the absence of seasonal phytoplankton blooms. The distribution of zooplankton both in space and time was somewhat paradoxical. A seasonal pulse of zooplankton was observed in spring and early summer and large standing crops were frequently found in the less productive regions of the ponds. Several possible explanations for these anomalous situations are considered. Relatively crude rates of exchange were computed for the pond system as a whole (9.4%/day) and for certain regions within the system. Land runoff entered the ponds chiefly in 2 regions. The nutrient contribution in runoff was small except for Green Hill Pond where high nitrate values in the fresh water effluents contribute to a higher standing crop of nitrate than elsewhere in the pond system. A method is described in which phosphate introduced into the ponds through the medium of exchange and runoff is used to compute the annual "net" production for the entire community. As an average for the system there is a daily accumulation of carbon in excess of the needs of the community amounting to 76 mg/m². The majority of this "net" community production occurs in the regions proximal to the breach, and under favorable conditions the surplus could be 374 mg/m² day. Problems of salt pond management for maximum sustained yield of economically important species are discussed. It is suggested that a certain ratio of exchange to runoff is necessary for optimal productivity in this type of environment and this ratio will be a function of tidal range, volume of the pond and fresh water head. Furthermore, it is probable that there is an optimal-sized pond for any given drainage basin which will yield maximum useful production.

Two major projects are suggested as economically feasible to improve conditions in this pond system, which would also serve as experimental tests for these hypotheses.

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THE TOMOCERINAE (COLLEMBOLA) IN OLD FIELD STANDS OF NORTH CAROLINA

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An investigation of the Tomocerinae was conducted in a selected series of old field successional stands in the Piedmont of North Carolina to determine the variability in size and trivial composition of populations in different seral stages of old field communities. An analysis of seasonal fluctuations in density and frequency of the several species was computed to decide what microclimatic factors affected each member of the subfamily; stratal sampling was employed to establish the possibility of vertical migrations in the litter-humus layer and underlying soil strata.

The Piedmont region of North Carolina presents an orderly secondary succession of vegetation following the abandonment of upland fields (Oosting 1942). Five types of old field communities were chosen for study with paired stations established for each successional stage with most stations located in the Duke University Forest (Figure 1). The author is grateful to Dr. I. E. Gray of the Department of Zoology, Duke University, for guidance and helpful criticisms, and to Dr. David Wray of the North Carolina Department of Agriculture for confirming the identifications of the Tomocerinae.

METHODS

Field work began on December 1, 1954 and was completed November 30, 1955. Sampling areas established in each stand were subdivided into 20 cm square quadrats. Six to 10 quadrats were extracted from each station every month,

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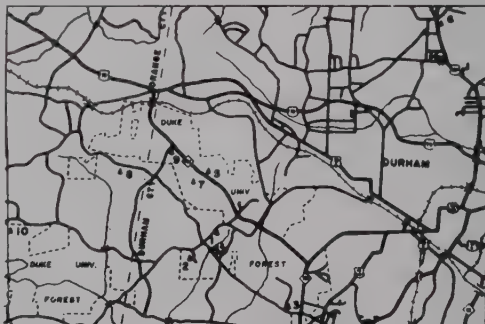


FIG. 1. Map of Durham and Orange Counties (in part) showing locations of stations studied. Exact location is indicated by solid triangle.

depending on areal extent of the stand. Samples were divided into 3 strata, (1) a surface stratum, including litter, fermentation and humus layers, (2) an upper soil stratum, containing a 2 inch layer of soil (51 mm), (3) a lower soil stratum, having the next 3 inches (77mm) of soil.

Litter and soil temperatures were recorded weekly using Taylor maximum-minimum recording thermometers (No. 5448). Litter and soil moisture percentage values were computed by comparing field and oven dry weights. Evaporation values in each stand were recorded with Livingston porcelain bulb atmometers. The Tomocerinae were separated from samples in a standard Tulegren apparatus according to the modification recommended by Haarlov (1947).

The 10 stations are characterized in the following list:

Station 1		Station 9	
Vegetation	Characteristics	blackjack oak (<i>Quercus marilandica</i>)	Age: 150 years
ragweed (<i>Ambrosia artemisiifolia</i>)	Age ² : 2 years	post oak (<i>Quercus stellata</i>)	Soil: Orange silt loam
wild aster (<i>Aster ericoides</i>)	Soil: White Store fine, sandy loam	red cedar (<i>Juniperus virginiana</i>)	Litter: scattered hardwood detritus 2 cm. deep
	Litter: none	dogwood	
		sourwood	
Station 2		Station 10	
broom sedge (<i>Andropogon virginicus</i>)	Age: 3 years	blackjack oak	Age: 130 years
hair-leaved dog-fennel (<i>Eupatorium capillifolium</i>)	Soil: Creedmore sandy loam	post oak	Soil: Iredell silt loam
	Litter: none	white oak	Litter: hardwood detritus, 4 cm. deep
		dogwood	
		red cedar	
Station 3		RESULTS	
loblolly pine (<i>Pinus taeda</i>)	Age: 25 years	<i>Microenvironmental differences</i>	
red gum (<i>Liquidambar styraciflua</i>)	Soil: White Store fine, sandy loam	Open Field Stage (Stations 1 and 2): Temperature values recorded weekly exhibited great differences throughout the annual cycle. Surface soil temperatures recorded at a 5 mm depth registered a minimum temperature of -8° C and a maximum reading of 12° C in late December, while early July values were highest with maximal temperatures of 57° C and minimal readings of 35° C. At a 75 mm depth, minimal temperatures were -8° C (maximal temperatures, 0° C) in late December with the highest temperature being 25° C (minimal reading, 20° C) in late July.	
dogwood (<i>Cornus florida</i>)	Litter: pine straw, 5 cm. deep	Moisture percentage values (expressed as % dry weight) were usually higher in surface soil strata (0.51 mm) than in subsurface layers (52-128 mm). Maximal values of 31% in late December and minimal values of 0.5% in early May were recorded in surface soil, but subsurface figures ranged from 22% in early January to 1% in early May. Evaporation values were high from May through August fluctuating between 130 and 265 ml of water loss per week, but were lower during the autumnal period (30 to 90 ml).	
Station 4		Young Loblolly Pine Stage (Stations 3 and 4): The lowest weekly temperature -3° C, was recorded in the litter stratum in late December (maximum temperature, 9° C). A maximal temperature of 31° C in Station 3 appeared in early August with a minimum temperature of 24° C, but maximal temperature was lower in Station 4 (27° C) and occurred in early June (minimum temperature, 24° C). Soil temperatures taken at a depth of 55 mm followed the same basic pattern for both stations and demonstrated less variability in maximum-minimum readings and weekly variation with a minimal temperature of 3° C in early February (maximum temperature, 7° C) and a maximal soil temperature of 26° C in mid-September, the minimum temperature being 24° C.	
loblolly pine	Age: 25 years		
red gum	Soil: Creedmore sandy loam		
dogwood	Litter: pine straw, 8 cm. deep		
black oak (<i>Quercus velutina</i>)			
Station 5			
loblolly pine	Age: 70 years		
red gum	Soil: Herndon and Alamance silt loam		
white oak (<i>Quercus alba</i>)	Litter: pine-hardwood detritus, 4 cm. deep		
sourwood (<i>Oxydendrum arboreum</i>)			
dogwood			
green ash (<i>Fraxinus pennsylvanica</i>)			
Station 6			
loblolly pine	Age: 75 years		
red gum	Soil: White Store sandy loam		
white oak	Litter: pine-hardwood detritus, 3 cm. deep		
northern red oak (<i>Quercus borealis</i>)			
red bud (<i>Cercis canadensis</i>)			
sugar maple (<i>Acer saccharum</i>)			
Station 7			
white oak	Age: 190 years		
southern shagbark hickory (<i>Carya carolinai-septentrionalis</i>)	Soil: Georgeville silt loam		
southern red oak (<i>Quercus rubra</i>)	Litter: hardwood detritus, 9 cm. deep		
dogwood			
sourwood			
Station 8			
white oak	Age: 140 years		
southern shagbark hickory	Soil: Cecil sandy loam		
dogwood	Litter: hardwood detritus, 9 cm. deep		
pignut hickory (<i>Carya glabra</i>)			
southern red oak			
maple leaf viburnum (<i>Viburnum acerifolium</i>)			

² Refers to the successional age from the time of abandonment of the old field.

Moisture percentage readings were derived from the 3 sampled strata every week. Litter moisture values in both stations underwent considerable fluctuation from week to week, but were definitely higher (averaging 80% to 140%) in the autumnal, hiemal and prevernal aspects, fluctuating between 20% and 90% during the vernal and aestival periods. Evaporation values remained high from April through early July averaging about 120 ml of water loss per week, but after mid-July readings averaged about 40 ml of water loss through mid-November.

Old Loblolly Pine Stage (Stations 5 and 6): Thermal trends were similar in old pine with lowest litter temperatures of -5°C and maximal values of 13°C in mid-February. In early May maximal litter temperatures of 34°C (minimum temperature, 13°C) occurred in Station 5, but did not occur until early August in Station 6 when a high of 27°C (minimum temperature, 23°C) was established. Minimal soil temperatures of 3°C in Station 5 and 4°C in Station 6 occurred during early February, maximum temperatures being 7°C and 11°C , respectively; maximal temperatures of 25°C were recorded in late July and early August, minimum temperatures averaging 23°C .

Prevernal litter moisture averaged 140%, vernal and aestival records averaged 50% until late July, but August through December was a period of slightly higher values averaging 70%. Upper and lower soil strata displayed smaller variations and lower percentages, but followed the same pattern as litter moisture with prevernal values averaging 25%, vernal and aestival percentages declining to 7% and late aestival-autumnal collections averaging 20% in both localities. Evaporation rates fluctuated between 39 ml and 195 ml from April through July with an average weekly loss of 110 ml; autumnal measurements continued until November with less variation and an average of 45 ml of water loss.

Climax Stage (Stations 7 and 8): Greater variation in environment existed between paired climax stands since Station 8 was situated on a north-facing slope and the vegetation was undisturbed by a fall hurricane, thus environmental factors exhibited considerably less weekly fluctuation in this stand. Lowest litter temperatures occurred in mid-December with minimal temperatures of -5°C and -3°C and maximal temperatures of 13°C and 11°C in Stations 7 and 8, respectively. In early April before trees were in full leaf, a maximal temperature of 35°C (minimal temperature of 2°C) was recorded in Station 7, but maximal litter temperatures in Station 8 did not

reach a peak until late July when a value of 28°C was recorded (minimal temperature, 21°C). Minimum soil temperatures were 3°C in early February in both stations (maximum temperatures, 7°C in Station 7, 5°C in Station 8), while the highest soil temperatures in late July reached 29°C (minimum temperature, 23°C) in Station 7 and 24°C (minimum temperature, 22°C) in Station 8.

In litter and soil, moisture percentage values exhibited similar trends in both communities, though higher moisture values prevailed in Station 8. Hiemal and prevernal data averaged 145% in the litter of Station 7 but nearly 200% in Station 8. Vernal-aestival readings averaged 48% and 62% in Stations 7 and 8 with autumnal readings averaging 70% in Station 7 and 84% in Station 8. Upper and lower soil moisture records were relatively close with averages of 40% in the hiemal-vernal period, 22% in the aestival and early autumnal interval and 32% for the late autumnal period in Station 7. Somewhat lower values of 28%, 10% and 22% were recorded for comparable periods in Station 8. Evaporation rates were slightly but consistently lower in Station 8; readings for both stations fluctuated between 23 ml and 163 ml of water loss per week with an average of 90 ml from mid-April through July and decreasing in autumn with a range of 9 ml to 82 ml and an average of 40 ml.

Prelimax Stage (Stations 9 and 10): Minimal temperatures of -5°C and -7°C (maximal temperatures, 11°C and 15°C) were recorded in Stations 9 and 10 in late December with highest temperatures of 32°C in Station 9 and 30°C in Station 10 (minimal temperature, -3°C) prevailing in late March and April before trees were in full leaf. Minimal soil temperatures of 2°C (Station 9) and 0°C (Station 10) occurred during mid-February, maximal temperatures being 10°C for both stations at this time. In mid-July maximal soil temperatures of 25°C were recorded, while minimal temperatures were 23°C in Station 9 and 21°C in Station 10.

In the litter, moisture percentage measurements averaged about 110% throughout the hiemal and prevernal interval, 35% in the vernal and aestival period and 65% in the autumnal season for both stands. Upper soil moisture values were higher than lower soil determinations, averaging 55% during the hiemal-prevernal period compared with 25% for lower soil strata. During the remainder of the collection cycle both strata recorded average values of 20% (upper soil) and 10% (lower soil) for the vernal-aestival interval and 40% and 15% during the autumnal period. Evaporation in pre-

climax areas ranged from 17 ml to 170 ml of water loss from April through July with an average of 110 ml, while fall values ranged from 3 ml to 79 ml with an average of 46 ml of water loss per week.

Frequency-density of fauna in seral stages

In most stations *Tomocerus flavescens separatus* was collected with greater frequency and density than any other member of the genus, being found in greater numbers and more evenly distributed in young and old pine stands excepting Station 5. Seasonal distribution indicated definite population increases in the autumnal period in pine stands and, excepting Station 7, collecting results exhibited a parallel trend in population values and seasonal distribution in hardwood areas. Though Station 9 was an unsuitable habitat for other species of *Tomocerus*, *T. flavescens separatus* was collected once in October.

In Stations 3 and 4 populations of *Tomocerus lamelliferus* were noticeably smaller than contemporary samples of *T. flavescens separatus*, but aggregations of *T. lamelliferus* outnumbered those of *T. flavescens separatus* in Station 5. In climax stands *T. lamelliferus* displayed considerable distribution and density in collecting results, exhibiting somewhat higher values than *T. flavescens separatus* in Station 7. Populations of *T. lamelliferus* increased in the vernal and autumnal periods of the year. *Tomocerus vulgaris* and *Tomocerus flavescens americanus* appeared sporadically in most stations, being more abundant in the vernal and autumnal intervals of the collecting period. Eggs and juvenile specimens of the Tomocerinae were isolated from the humus layer of litter samples in every station excepting Station 9, being more abundant during the less favorable aestival and mid-hiemal seasons of the year. Juveniles of *T. flavescens separatus* and *T. lamelliferus* were isolated from the humus layer, the former species being more abundant in the fall and the latter often found in aestival samples. Juvenile specimens of *T. vulgaris* were collected in Station 8 during September and October.

Species association with seral stages

Data presented in the following 2 x 2 contingency tables (Table I) reflects the associational tendencies of the various species for different stations. Chi-square values in paired pine stands for *T. flavescens separatus* were statistically insignificant, however the species showed a very definite preference for young pine stands ($\chi^2 = 17.4$). In hardwood areas statistically significant

TABLE I. Associational analysis of collection data and vegetational cover type for the litter-humus stratum

<i>Tomocerus flavescens separatus</i>				
	Quadrats With	Quadrats Without	Total	χ^2
Young Pine.....	97	109	206	17.4
Old Pine.....	48	136	184	
Total.....	145	245	390	
Station 7.....	8	88	96	20.9
Station 8.....	33	55	88	
Total.....	41	143	184	
Station 9.....	2	94	96	22.4
Station 10.....	19	47	66	
Total.....	21	141	162	
Climax.....	41	143	184	4.4
Prelimax.....	21	141	162	
Total.....	62	284	346	
Pine.....	145	245	390	32.6
Hardwood.....	62	284	346	
Total.....	207	529	736	
<i>Tomocerus lamelliferus</i>				
Station 3.....	30	66	96	14.7
Station 4.....	10	100	110	
Total.....	40	166	206	
Station 5.....	33	63	96	34.5
Station 6.....	0	88	88	
Total.....	33	151	184	
Station 7.....	17	79	96	9.0
Station 8.....	34	54	88	
Total.....	51	133	184	
Climax.....	1	133	184	50.4
Prelimax.....	0	162	162	
Total.....	51	295	346	
<i>Tomocerus flavescens americanus</i>				
Young Pine.....	22	184	206	9.9
Old Pine.....	4	180	184	
Total.....	26	364	390	
Station 7.....	1	95	96	5.8
Station 8.....	9	79	88	
Total.....	10	174	184	
<i>Tomocerus vulgaris</i>				
Station 3.....	2	94	96	4.1
Station 4.....	11	99	110	
Total.....	13	193	206	
Climax.....	10	174	184	5.0
Prelimax.....	1	161	162	
Total.....	11	335	346	

figures prevailed in comparing equivalent stages with an indication of greater association in Stations 8 and 10 and an affinity for climax rather than preclimax areas. *Tomocerus flavescens separatus* demonstrated a very definite association with pine communities ($\chi^2 = 32.6$).

Analyses of association among litter samples of *T. lamelliferus* in paired coniferous communities reflects a definite affinity for Station 3 and 5, but no significant value ($\chi^2 = 0.05$) in comparing the fauna of young and old pine stands. The organism was present in greater numbers of samples in Station 8 than in the paired climax area. Since no specimens were found in litter samples in preclimax stands, statistical analysis yields significant values indicating a greater degree of association with climax areas. A comparison of coniferous and hardwood collections yielded insignificant χ^2 values.

Data compiled for litter samples of *T. flavescens americanus* revealed no affinity among paired coniferous stands, but a preference for young pine stands ($\chi^2 = 9.9$). Figures of statistical significance were derived when collecting results from the 2 climax stands were compared ($\chi^2 = 5.8$), *T. flavescens americanus* being far more abundant in Station 8 which served as a more favorable environment. Sparsity of distribution in preclimax areas rendered no results of statistical significance when the 2 communities were compared. Chi-square values were insignificant when comparing climax with preclimax communities ($\chi^2 = 2.0$) and pine with hardwood stands ($\chi^2 = 2.9$). Tests of association for *T. vulgaris* among paired stands indicates only one instance of statistical significance ($\chi^2 = 4.1$) when collection results of Stations 3 and 4 were compared with a definitely higher degree of association for Station 4. An analysis of results in other paired stands indicated greater association for Stations 5, 8 and 10, though statistical results were not significant. When climax stands were compared with preclimax areas the species revealed an affinity for climax stands ($\chi^2 = 5.0$), however a comparison of pine and hardwood areas yielded results of no statistical significance.

Soil populations were confined to the upper soil stratum but quantitative results were so sparse that when resorting to Yates' correction for continuity only one species (*T. lamelliferus*) presented a significant chi-square value; however the following indications were evident. *Tomocerus flavescens separatus* was in more old pine quadrats than young pine plots and exhibited a greater distribution in upper soil of pine stands than hardwood communities. *Tomocerus lamelli-*

ferus was found in greater numbers in old pine communities. A comparison of climax and preclimax upper soil samples yielded results of statistical significance with definite association for climax communities; more hardwood samples contained the species when compared with pine communities. *Tomocerus flavescens americanus* was recovered from only 2 upper soil samples of young pine stands and *T. vulgaris* appeared in 2 climax upper soil samples.

DISCUSSION

A review of the literature indicates that the Tomocerinae exist only in areas with a definite litter stratum or a litter-like environment, i.e., grass prairie communities. Shackleford (1929) found *T. flavescens americanus* in low prairie grass of central Illinois during the autumnal and hiemal seasons and in high prairie grass throughout the year. Cameron (1917) collected *Tomocerus tridentiferus* in shallow litter at the edge of a pasture in Cheshire, England. Smith (1928), Bird (1930) and Bellinger (1954) found that in a successional series of stands, there was a tendency for the Tomocerinae to become more abundant and to exhibit a more constant annual distribution in communities with a thicker litter stratum. Pearse (1943) collected *T. flavescens* and *Tomocerus* sp. in the control plots of a 31-year-old loblolly pine stand in Duke Forest, but never in plots where litter was removed by raking or burning. Heyward and Tissot (1936), comparing burned and unburned regions of long leaf pine in Florida, discovered that the number of Collembola was drastically reduced in burned areas. In open field communities sampled during this investigation, lack of litter prevented the establishment of *Tomocerus*, however according to Bellinger *Tomocerus* became established after pine had been introduced and formed a thin litter around each tree. In the present study pine and hardwood communities possessed a litter stratum adequate for the establishment of the Tomocerinae. A sparsity of trees in preclimax stands yielded a thinner scattered litter resulting in decreased density-frequency and annual distribution when compared with other forested areas.

The importance of moisture was stressed by Davidson (1936) who stated that (p. 88): "Although temperature has been widely used as an index to the distribution and seasonal activity of insects, ecological studies during the past fifteen years or so have abundantly demonstrated the importance of moisture, and shown that temperature alone cannot be considered as an adequate climatic index for this purpose." Investigations of col-

lemnolan populations in open fields on the European continent by Dogel (1924) in Russia, Frenzel (1936) in Germany and Weis-Fogh (1948) in Jutland revealed that population size was dependent on moisture conditions prevalent in the environment. In England various types of open fields, including pastures and cultivated areas, were investigated for Collembola and mites by Morris (1920, 1922, 1927), Ford (1935, 1937, 1938), Glasgow (1939), Salt *et al.* (1948) and others, with the general conclusion that moisture content of the soil controlled population growth. (Faunal analyses were unanimous in their omission of *Tomocerus* in British and continental studies of open field communities.

A comparison of collembolan populations in young and old pine stands (Figure 2) revealed a very marked decrease in density and distribution of the Tomocerinae in older stands. Moisture percentage values in litter displayed greater amplitude from week to week in older loblolly pine

stands (Stations 5 and 6) than in younger coniferous areas (Stations 3 and 4). *Tomocerus* failed to adjust to such sudden changes in moisture over short periods of time, consequently such events resulted in decreased density and distribution in older coniferous stands. Some overstory trees (oak and hickory) were lost in Station 7 during a fall hurricane; removal of these trees the following spring introduced considerable differences in the microenvironment when compared with the paired, undamaged stand (Station 8). Both climax communities possessed litter of equivalent depth and composition, however litter in Station 7 was exposed to greater environmental extremes due to reduction in forest canopy. Moisture percentage data were proportionally lower for Station 7 than for Station 8 over equivalent time periods. In preclimax stations moisture conditions were more adverse for the Tomocerinae since increased insolation and spar-

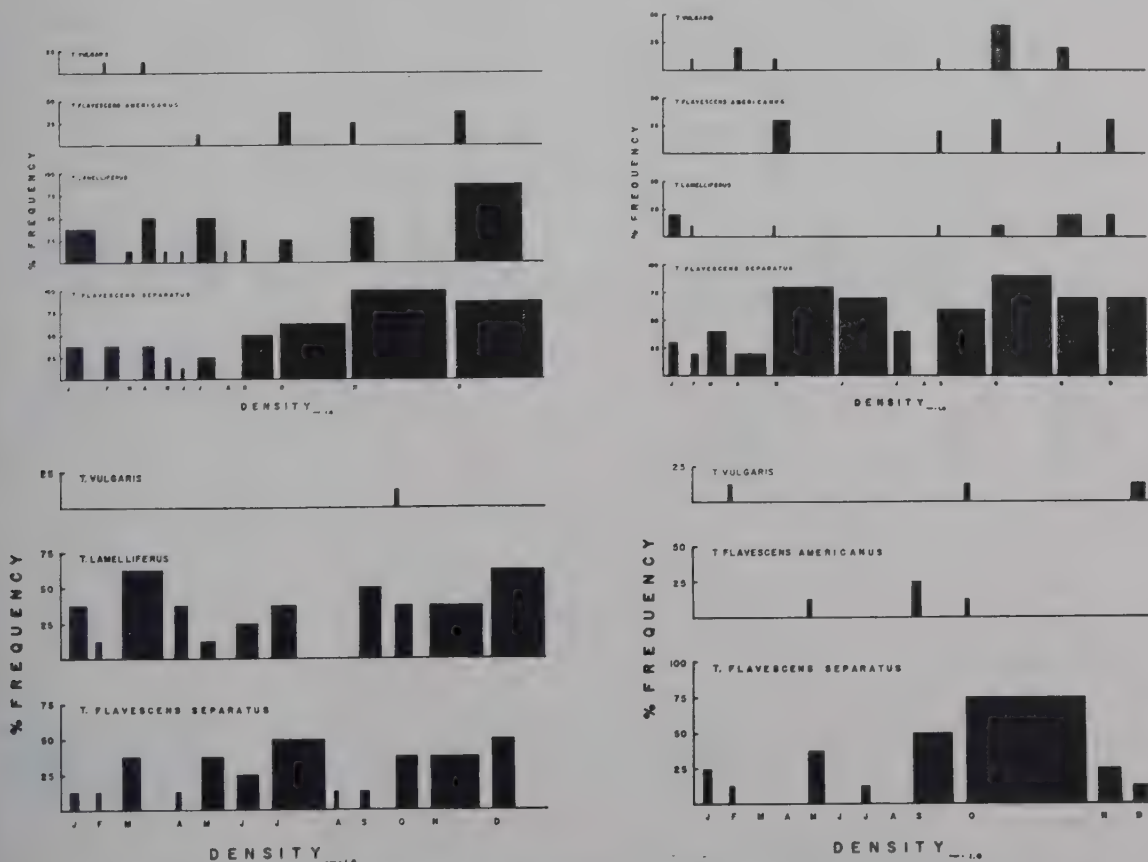


FIG. 2. Frequency-density diagram of the Tomocerinae present in monthly litter samples of pine stands. Upper left: Station 3, upper right: Station 4, lower left: Station 5, lower right: Station 6.

sity of hardwood litter yielded wide ranges of moisture percentage values.

Tomocerus flavescens separatus and *T. lamelliferus* were dominant species in coniferous communities with increases in frequency and density occurring during the autumnal and early hiemal periods. Reduction in thermal values and increases in litter moisture were indicative of favorable microclimatic conditions for both species. In terms of density and frequency in coniferous communities, *T. flavescens americanus* and *T. vulgaris* were sparsely represented with population patterns indicating that both species were far removed from optimal conditions, populations arising only when climatic conditions approximated minimal requirements for the organism.

The cryptozoa of an Illinois oak-hickory forest was studied by Cole (1946). *Tomocerus* and *Entomobrya* were the most common genera in this ecological niche with populations of both genera higher during the moister part of the year (early fall). In an elm-maple forest in Illinois investigated by Blake (1931), *T. flavescens* was present

from early March to mid-June and underwent fluctuations in keeping with moisture and temperature differences, decreasing as temperatures increased and moisture values declined in the litter stratum. Bohnsack (1954), in a study of the forest floor arthropods of an oak-hickory woodland in southern Michigan, found that *T. flavescens* and *T. lamelliferus* exhibited greatest density in April, May, June and September.

Collection results in hardwood areas are in agreement with past literature. *Tomocerus flavescens separatus* and *T. lamelliferus* were the dominant species present in hardwood communities, with larger populations in Station 8 than any other stand because of the more adverse microclimatic conditions prevalent in Station 7 and preclimax areas. Both species exhibited very drastic frequency-density increases during the autumnal and early hiemal seasons in both climax stations (Figure 3) paralleling collection results in coniferous communities, but underwent a decline in frequency and density during the hiemal, vernal and aestival periods with periodic fluctua-

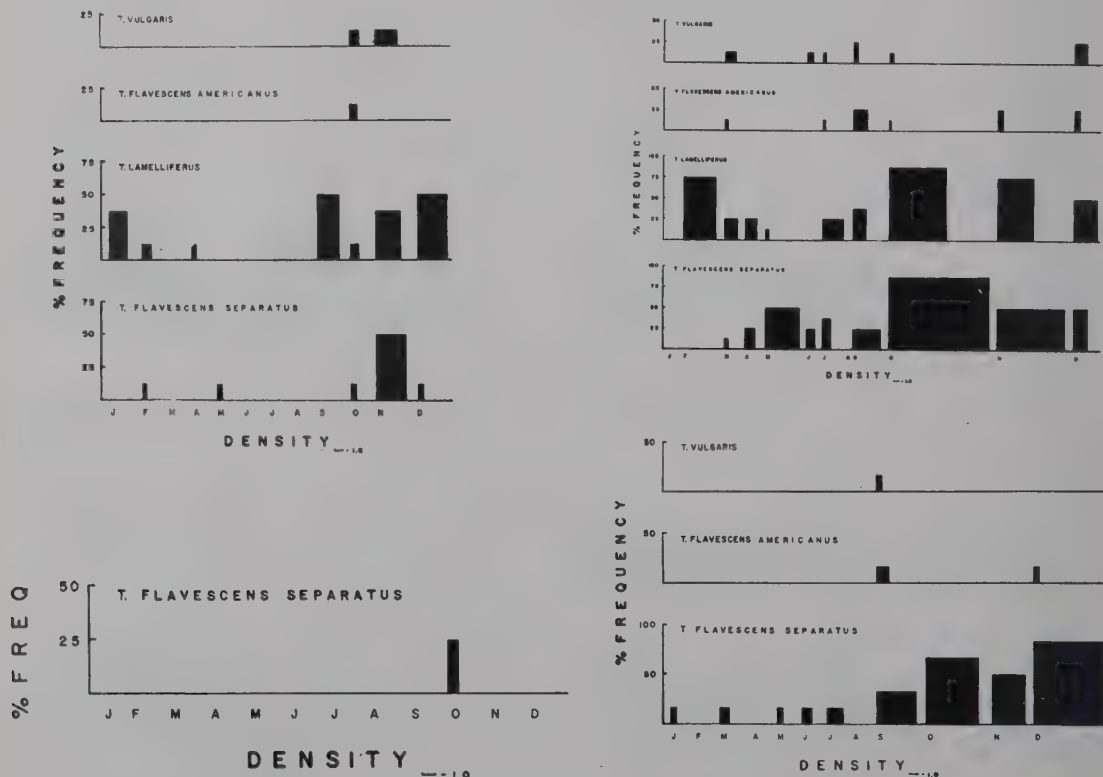


FIG. 3. Frequency-density diagram of the Tomocerinae present in monthly litter samples of hardwood stands. Upper left: Station 7, upper right: Station 8, lower left: Station 9, lower right: Station 10.

tions which closely paralleled microclimatic conditions (temperature and moisture). Increased moisture resulted in population increases; *T. lamelliferus* was more sensitive to moisture changes, requiring an environment of higher humidity than *T. flavescens separatus*. *Tomocerus lamelliferus* never appeared in any preclimax collection, but *T. flavescens separatus* was present in greater numbers and frequency than any other organism. The presence of *T. flavescens separatus* in Station 9 and the higher frequency-density values for the species in Station 10 (Fig. 3), substantiates the hypothesis that this organism is more tolerant of adverse microclimatic conditions than other members of the genus. Population trends in preclimax communities were similar to those in climax and coniferous areas, though densities and frequencies for *Tomocerus* were reduced in accordance with a more adverse environment.

Tomocerus flavescens americanus and *T. vulgaris* appeared sporadically and in very small numbers throughout the collecting period in hardwood areas. A more favorable microenvironment in Station 8 resulted in a greater annual distribution of both species than in Station 7. Microenvironmental conditions were not adequate in Station 9 for the appearance of either species, but both organisms were present in Station 10, though they were sparsely distributed and population size was minimal.

The Tomocerinae, when found, were always in the upper 5 mm of soil in soil samples (Figures 4 and 5). *Tomocerus flavescens separatus* and *T. lamelliferus* were the most common representa-

tives; *T. vulgaris* was found in one locality (Station 8) in September and October, but *T. flavescens americanus* was never found in this stratum. Sparse populations of *Tomocerus* in soil were caused by the lack of structures enabling them to burrow into soil and requiring them to move along channels provided by other organisms. Such passages had to be relatively large since the Tomocerinae are larger than most Collembola. The microclimate of the soil, though not susceptible to rapid changes, exhibited moisture conditions somewhat removed from the optimal range for *Tomocerus*. Moisture percentage figures in coniferous upper soil strata inhabited by *Tomocerus* ranged from 4 to 47%, while weekly temperatures ranged from 5° to 26° C. In hardwood communities moisture percentages were somewhat higher with a range of 13 to 57% and a weekly temperature range running from 3° to 26° C. Soil populations were small and poorly distributed, most specimens being immature. *Tomocerus lamelliferus* was the only species collected as an imago in any quantity. This indicated that during periods of unfavorable microenvironmental conditions some species attempt to move into the upper soil to deposit eggs and, as favorable microclimatic factors evolve, eggs hatch and immature organisms move up to the humus stratum of the community. Wallwork (1959) has observed vertical migrations of this nature while working with mites and collembolans in a hemlock-yellow birch stand at Imp Lake, Michigan.

Recent work published by Stevanovic (1956) on several forest types in the vicinity of Kopaonik, Russia in 1953 and 1954 cites the presence of *T.*

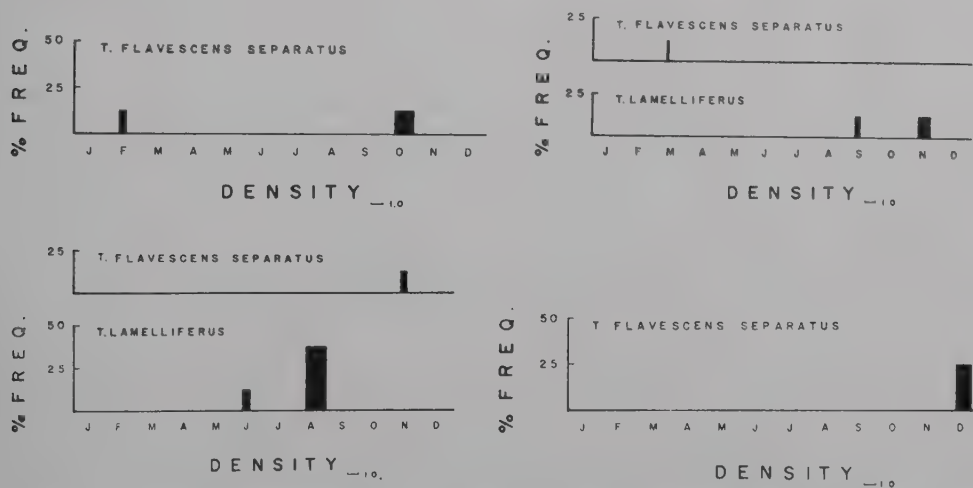


FIG. 4. Frequency-density diagram of the Tomocerinae present in monthly upper soil samples of pine stands. Upper left: Station 3, upper right: Station 4, lower left: Station 5, lower right: Station 6.

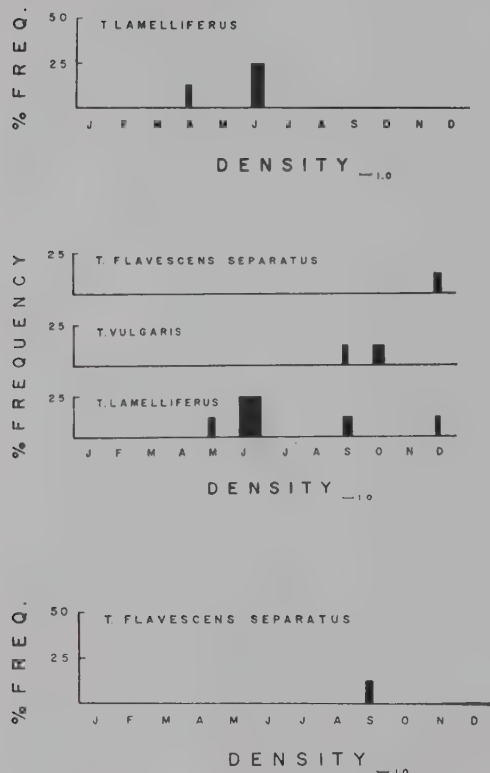


FIG. 5. Frequency-density diagram of the Tomocerinae present in monthly upper soil samples of hardwood stands. Top: Station 7, middle: Station 8, bottom: Station 10.

vulgaris in litter of a beech-woodrush, (*Fageto-Lusuletum pauperum*) association. *Tomocerus vulgaris* was collected when temperatures were between 2.91° C and 14.18° C and rainfall varied from 59.3 mm to 110.0 mm, though mean monthly temperatures ranged from -22.00° C to 14.18° C and rainfall varied between 12.2 mm and 166.7 mm per month. Litter-humus temperatures in the present investigation varied from -6° C to 35° C in wooded communities. *Tomocerus flavescens separatus* maintained relatively high populations over a weekly temperature range of -3° C to 27° C, but if litter temperatures exceeded 29° C, populations decreased rapidly and were very small as temperatures increased above 31° C. Populations of *T. lamelliferus* exhibited similar trends, though large populations were recovered in areas where weekly temperature values were as low as -6° C. *Tomocerus flavescens americanus* and *T. vulgaris* were collected in smaller numbers and frequencies from all forest communities.

Populations of moderate size were recovered when litter-humus temperatures ranged between 11° C and 26° C; if temperatures decreased to -3° C or increased to 31° C, populations decreased in size with higher temperatures accounting for more rapid decreases.

The largest populations of *T. flavescens separatus* were recovered when weekly litter-humus moisture percentages varied between 49 and 112%, but as the amplitude of readings increased there were corresponding reductions in the size of populations; decreases were slight since moisture values ranging from 3 to 370% were satisfactory for the maintenance of moderate populations. *Tomocerus lamelliferus* was present in greatest numbers when moisture figures varied from 66 to 112%, but decreased as moisture percentage readings fluctuated beyond these values. This species was never collected when records were below 6% or above 200% in coniferous communities, or when values were below 16% or above 320% in deciduous stands. *Tomocerus flavescens americanus* and *T. vulgaris* were recovered in moderate numbers from coniferous areas when percentage figures ranged between 6 and 160% and 64 to 160%, respectively. If percentage figures decreased below 45%, populations declined rapidly; smaller populations of these species were recovered in deciduous communities since microclimatic values exhibited greater fluctuations for equivalent periods.

SUMMARY

1. The growth and decline of populations of the Subfamily Tomocerinae (Order Collembola) in a successional series of old field stands in the Piedmont region of North Carolina were traced throughout the various seasonal periods of an annual cycle using 5 types of old field communities for the study with duplicate stations for each community type. The successional ages were: open fields abandoned for several years with wild aster and broom sedge as dominant vegetation (Stations 1 and 2), 15-year-old loblolly pine stands (Stations 3 and 4), 50- to 60-year-old loblolly pine forest (Stations 5 and 6), climax communities with oak-hickory flora (Stations 7 and 8) and preclimax stands of blackjack and post oak (Stations 9 and 10).

2. Random 20 cm square quadrats were subdivided into litter, upper soil and lower soil strata and sampled in paired units from stations every month. Specimens were separated from stratal samples in a modified Tullgren funnel. Recorded environmental data included weekly records of maximum-minimum temperatures, evaporation rate and moisture percentage values.

3. No specimens of the Tomocerinae inhabited any stratum of open field stands. Forested communities contained *T. flavescens separatus*, *T. lamelliferus*, *T. flavescens americanus* and *T. vulgaris* in the litter-humus and the first few millimeters of the upper soil strata, but no member of the subfamily was found in the lower soil stratum. In terms of frequency and density the largest populations occurred in the autumnal and early hiemal periods.

4. *Tomocerus flavescens separatus* and *T. lamelliferus* were recovered in greater numbers and frequency than other trivial forms of the subfamily. Population trends in climax communities tended to follow patterns which were very similar to those established for coniferous communities with smallest populations appearing in preclimax stands where sparsity of litter yielded an unstable microenvironment with more severe fluctuations in the microhabitat. One preclimax stand (Station 9) possessed only one species, *T. flavescens separatus*, and was the only wooded station with no Tomocerinae in the upper soil stratum. The presence of this species in an environment which would not accommodate other members of the subfamily indicated a greater tolerance for moisture and temperature conditions. *Tomocerus lamelliferus* was collected in small numbers in the immature and imago stages in the upper soil, but other trivial forms were found in this stratum as eggs or immature specimens.

5. Tests of association (chi-square) in litter-humus samples indicated that *T. flavescens separatus* exhibited a definite affinity for coniferous areas with a definite preference for young pine stands, while *T. lamelliferus* did not display similar tendencies. *Tomocerus flavescens americanus* was associated with young pine areas rather than old pine, most other comparisons yielded insignificant values. *Tomocerus vulgaris*, as was true of all other trivial forms, showed an affinity for climax rather than preclimax vegetation, but in other respects tests of association were statistically insignificant.

6. Multiple physical factors extant in the microclimate exerted a very definite influence on population size; moisture and temperature values had a profound affect on the Tomocerinae.

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MASS MORTALITY OF A MARINE FAUNA FOLLOWING TROPICAL RAINS¹

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INTRODUCTION

Mass mortalities among marine animal communities are well known in certain parts of the world and result from one or more of a variety of environmental factors such as temperature or salinity changes, or "red tide" (Brongersma Sanders 1957), but few authentic cases are on record of such mortalities being caused by a reduction in salinity of the water. Beaven (1946) found evidence that oyster mortalities on 6 occasions in Chesapeake Bay coincided with heavy runoff from the Susquehanna river and consequent reduced salinities over the oyster reefs. Collier and Hedgpeth (1950) describe the flooding of Texas rivers leading into enclosed bays on the Gulf coast, and state: "Virtually nothing is yet known . . . of the biological effects of these floods, except that oyster reefs in the inner bays may be occasionally wiped out." Hill and Webb (1958) have described the annual flooding of Lagos Harbor in Nigeria and the destruction of its marine fauna. Sandison and Hill (1959) described the subsequent recolonization of this harbor. Thorson (1946) records that in fjord regions of east Greenland in June the melting ice forms a brackish water layer on the surface which kills all animals along the coasts down to a depth of 3 to 5 metres. Finally, MacGinitie (1939) describes a single instance in which the Santa Ana River in California overflowed into Newport Bay and killed large numbers of sessile organisms.

The present paper describes 3 separate instances of mass mortality among sessile marine animals in Kingston Harbor, Jamaica following heavy rain storms. The evidence available at present suggests that river flooding is not necessarily the only cause of the disaster but that in an enclosed mangrove lagoon the runoff from the mangroves themselves is also of importance in killing animals attached to the mangrove roots.

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GEOGRAPHY AND TOPOGRAPHY

Kingston Harbour is situated on the south coast of Jamaica at 17° 58' N., 76° 48' W. (Figure 1). It forms an extensive natural harbour 10 miles long and about 1.75 miles wide along most of its length (Figure 1), bounded on the north, west and east by the mainland mass and on the south by a narrow tongue of land seldom more than one tenth of a mile wide except at Palisadoes Airport. The northern shore is dominated by the city of Kingston and its attendant docks and, in the northwestern corner, there is a shallow arm to the harbor, Hunt's Bay, roughly 2.25 miles long and 2 miles wide. Two rivers, the Rio Cobre and the Ferry River both discharge into Hunt's Bay; outside the rainy season the flow of these rivers is limited and does not reduce the harbour water below 35 ‰. In the rainy season, however, the rivers are liable to extensive flooding, but salinity determinations throughout the harbor and observation from high ground of the turbid waters both indicate that the flood waters usually flow along the western side of the harbor out to sea and do not circulate around the harbor to any great extent. In strong westerly winds the flood waters may be carried to the east into the harbor. There are extensive mangrove swamps on the western side of Hunt's Bay and also on the southern shore between Palisadoes Airport and Port Royal at the harbor entrance. The harbor entrance in the south-west corner is almost

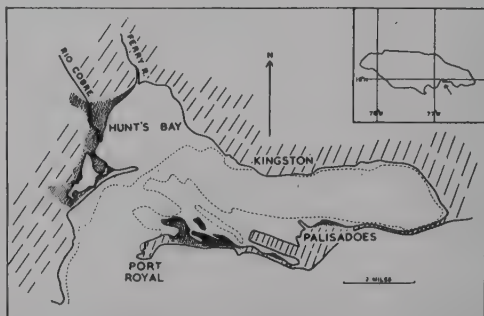


FIG. 1. Map of Kingston Harbor, Jamaica. Stippling indicates areas of mangrove swamp. Broken line indicates approximate limits of 5.5 metre (3 fathom) depth contour. Inset, map of Jamaica showing position of Kingston Harbor indicated by arrow.

2 miles across and is the only place where extensive interchange occurs between the harbor water and the open sea.

Except for the narrow ship channel the western end of the harbor is relatively shallow (Fig. 1) but at the eastern end it opens out into a broad deep basin of relatively uniform depth (15 to 20 metres). Throughout most of the year strong sea breezes blow from east to west along the harbor during the day; it seems probable that these winds set up a water circulation carrying surface water from the eastern end toward the mouth of the harbor and that this is replaced by a deeper current flowing up the channel and so into the eastern basin. The normal daily tidal range within the harbor is 23 centimetres.

The mangrove area

Most observations on mortality were made in mangrove swamp lying to the east of Port Royal (Figure 2). To the east of Port Royal is the wide Port Royal lagoon in the south-west corner of which is a narrow channel, Station A, seldom more than knee deep and about 2 metres across, which runs through the mangroves, under a main road and connects to a small lagoon between the road and the outer beach. At the eastern end of the Port Royal lagoon a channel of varying width runs through the mangroves and connects to another lagoon, Fort Rocky lagoon (F in Fig. 2). The latter opens into the main harbor across a shallow bar at the north-west corner and on its southern shore there is another channel, Station B, similar to Station A joining to another small lagoon between the road and outer beach. Salinity in these lagoons is normally about 35 ‰.

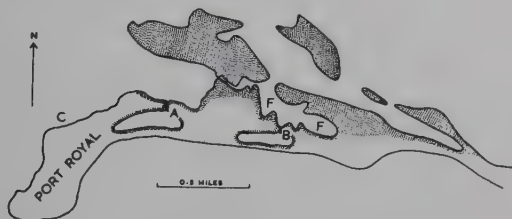


FIG. 2. Map of mangrove area to east of Port Royal, Jamaica, showing sampling stations A, B and C. F = Fort Rocky lagoon. Stippling indicates approximate distribution of mangrove.

The lagoons and their channels are bordered by extensive mangrove swamp and at the water's edge long mangrove roots hang down freely into the water and are easily raised in the hand for inspection. These roots become clothed with a dense mass of sedentary organisms including many species of sponges, actinians, annelids, cir-

ripedes, lamellibranchs, bryozoans and ascidians, and among these there also develops a community of errant animals such as nereid polychaetes, various crustaceans, gastropods and echinoderms (echinoids, asteroids, ophiurans and synaptid holothurians). In the shallow waters at Stations A and B there are, in addition to the mangrove root communities, many sedentary and errant forms living in and on the gravel floor.

RAINFALL

The average annual rainfall at Palisadoes Airport is 780 mm (based on data for the period 1942-1957) and the bulk of this is distributed between 2 rainy seasons one in April or May and the other in September or October, but considerable variation may occur from year to year (Table I). In considering the effect that any rainy season may have on the salinity of the harbor waters and consequently upon its animal life 2 principal factors have to be considered. Firstly the total amount of rain is not so important as its distribution in time; a certain amount of rain spread evenly over 10 days will have far less effect than if the same amount is concentrated into 2 or 3 days. Secondly the salinity of the harbor waters is affected from 2 different sources, direct rainfall onto the harbor and its immediate drainage (*i.e.* mangroves) and rainfall into the catchment area of the Rio Cobre and Ferry River and consequently the flow of water from these rivers into the harbor.

In the 4 years 1956-59 inclusive 3 mass mortalities have occurred: one in October 1956, one in May 1958 and one in October 1958. Table I shows the monthly rainfall figures at Palisadoes Airport for these 4 years, together with the maximum precipitation in a 24-hour period during each month. It will be seen that the 3 mass mortalities coincided with the only months in which total precipitation exceeded 300 mm and the maximum for a 24 hour period exceeded 100 mm.

In Table II the rainfall in each of the 3 critical periods preceding mass mortality are shown together with the averages of 5 localities in the water catchment area of the Rio Cobre. In 1956 the bulk of the rain fell in 2 days (13th and 14th October), in May 1958 it lasted for 5 days (18th to 22nd) with a lull on the 2nd day, and in October 1958 the bulk fell within 3 days (3rd to 5th).

The effect of these sudden heavy rainfalls and the subsequent drainage from mangrove and river is to produce a layer of low salinity water which spreads out across the harbor and its lagoons. Being less dense, this remains as a surface layer

TABLE I. Monthly rainfall in millimetres, and maximum rainfall in one day in each month at Palisadoes Airport, Jamaica in the years 1956-1959 inclusive. The average annual total for the years 1942-1957 inclusive is 780 millimetres

	1956		1957		1958		1959	
	Total	Max/Day	Total	Max/Day	Total	Max/Day	Total	Max/Day
January.....	2	2	2	2	77	32	6	2
February.....	42	26	9	4	0	0	11	11
March.....	13	4	27	14	0	0	7	3
April.....	53	39	80	65	5	3	33	11
May.....	28	22	148	68	398	121	114	59
June.....	30	6	6	2	137	27	4	4
July.....	130	52	14	12	27	8	10	6
August.....	9	4	17	11	31	17	2	1
September.....	11	4	141	85	48	20	13	12
October.....	330	195	109	59	302	156	138	36
November.....	48	39	4	2	66	38	102	40
December.....	3	2	0	0	7	6	17	6
Annual Total.....	699		557		1098		457	

TABLE II. Rainfall in millimetres at Palisadoes Airport and in the catchment area of the Rio Cobre in 3 periods preceding mass mortalities. The river catchment data are the averages for 5 rain-gauge stations

	12th to 15th Oct. 1956	17th to 22nd May 1958	2nd to 7th Oct. 1958
Palisadoes Airport.....	214	360	287
Catchment Area.....	195	236	340

floating above the more dense high salinity harbor water. The effect on the animal life is dealt with separately for each period in the following sections.

THE 1956 MORTALITY

Between 12th and 15th October 214 mm of rain fell in 72 hours; 195 mm of this fell in one 24 hour period. The mangrove area was not visited until 17th October by which time many sedentary animals had been killed particularly in the upper 30 cm of the surface layers, while some delicate species had been killed down to a depth of 60 cm. The most seriously affected forms appeared to be social and colonial ascidians (*Ecteinascidia turbinata*, *Perophora bermudensis*, *Clavelina oblonga*); among solitary ascidians *Rhodospoma turcicum* had been killed extensively but *Herdmania momus* and *Microcosmus exasperatus*, species with tough tests, had survived in places. Balanoid barnacles had survived well even close to the surface. A sample mangrove root had 77% of all animals dead in the top 30 cm and only 24% dead in the next 30 cm from the surface. At the edge of the Fort Rocky lagoon, in a rapid survey of a piece of water less than 50 cm deep and about 20 sq metres in extent with a coarse sand bottom,

22 sipunculoids, 5 holothurians and 3 echinoids (*Lytechinus variegatus*) were picked up dead. Similarly, in a 10 metre stretch of the channel at Station B, 3 nereid worms, 15 ophiuroids, 9 holothurians, 9 asteroids (*Echinaster echinophorus*) and 1 echinoid (*L. variegatus*) were found dead and no living specimens were found.

A similar effect was noticed on experimental panels suspended from a raft at Port Royal (Station C). The water here is 8 metres deep and the panels, used for studies of *Ascidia nigra*, were suspended so that their upper edge was 37 cm below the surface. Except for balanoids everything was dead on the top 30 cm of the panels leaving a well defined line of demarcation between living and dead. As the rafts rise and fall with the tide this provides a good measure of the depth to which salinity was lowered sufficiently to cause death, in this case 67 cm below the surface.

Table III shows surface salinities at 3 places subsequent to this mortality. The lowest value found was 11.4 ‰ 3 days after the rain.

TABLE III. Surface salinities at 3 localities in the mangrove area after the rains in October 1956. Figures are given in parts per thousand

	17th Oct.	23rd Oct.	1st Nov.	17th Dec.	24th Jan.
Fort Rocky Lagoon.....	11.4	—	—	—	33.8
Station B.....	17.3	—	23.9	34.5	34.7
Station C.....	20.4	34.1	34.0	35.4	34.8

THE MAY 1958 MORTALITY

Heavy rain fell all day on 18th and morning of 19th May and again from the night of 20th to

1600 hrs on 22nd. At Palisadoes 360 mm of rain fell in the whole period with a 24 hour maximum of 121 mm on 18th. Throughout the river catchment area values averaged rather less (236 mm).

Table IV shows surface salinities at various places both during and after the rain. The lowest values were obtained on 22nd May shortly after the cessation of the rain and in most cases had risen again to values over 30 ‰ by 27th. Minimum values were 13.3 ‰ at the edge of Fort Rocky lagoon and 17.0 ‰ at Station B.

TABLE IV. Surface salinities in the mangrove area in May and June 1958. Figures are given in parts per thousand. Samples taken before and after mid-day at Station C. (Port Royal) have been separated (see text). The value of 13.3 in Fort Rocky lagoon was obtained near the edge of the lagoon; the other samples were from the lagoon centre.

	19th May	21st May	22nd May	23rd May	24th May	27th May	3rd June	14th June
Station A.....	34.1	24.9	25.8	23.1	27.0	31.6	—	—
Station B.....	28.9	18.5	17.0	19.7	25.2	30.7	—	—
Station C (A.M.).....	—	—	29.9	—	—	—	31.0	26.0
Station C (P.M.).....	35.7	22.6	—	—	33.6	33.6	35.1	34.9
Fort Rocky Lagoon.....	—	—	13.3	28.5	—	32.5	—	—

During a lull on 21st May a rapid survey showed that only the colonial ascidian *Polyclinum constellatum* was seriously affected. A further check at Stations A and B just after the rain ceased on 22nd showed little mortality except of *P. constellatum* and some holothurians. On 23rd holothurians and sabellid worms were also dead at Stations A and B and *Echinaster echinophorus* and *Lytechinus variegatus*, although still alive, were clearly weakened as they failed to right themselves when turned upside down. The alcyonarian *Telesto* sp. and a large sand anemone *Phyllactis flosculifera* had both survived.

In Fort Rocky lagoon on mangrove roots sponges and ascidians were all dead but the oyster *Isognomon alatus* had survived. There was no unusual mortality on the rafts at Station C.

TABLE V. Surface salinities in the mangrove area October 1958 to January 1959. In Fort Rocky Lagoon, except on 8th October, samples were taken at 3 points and the figures given are the averages of these; on 8th October the figure of 5.4 ‰ was obtained near the east end of the lagoon. Samples taken before and after mid-day at Station C (Port Royal) have been separated (see text)

	5th Oct.	6th Oct.	8th Oct.	9th Oct.	18th Oct.	6th Nov.	13th Nov.	9th Dec.	10th Dec.	9th Jan.	15th Jan.
Station A.....	—	24.3	25.4	—	—	29.8	—	34.7	—	—	—
Station B.....	28.5	25.7	16.5	—	23.0	29.1	—	32.6	—	34.6	—
Station C (A.M.).....	—	24.4	27.9	—	24.5	27.0	30.4	—	—	—	30.9
Station C (P.M.).....	35.0	—	34.6	34.8	34.3	32.8	32.7	—	33.6	—	35.8
Fort Rocky Lagoon.....	—	—	5.4	—	25.7	28.8	—	32.8	—	34.5	—

THE OCTOBER 1958 MORTALITY

A period of rain lasted from 2nd to 7th October, the heaviest falls being on 4th to 6th with a maximum at Palisadoes of 156 mm on 5th. Palisadoes had a total fall of 287 mm but values as high as 400 mm occurred in the river catchment area where the average was 340 mm.

Table V shows surface salinities in the mangrove area following these rains. Values as low as 5.4 ‰ were recorded in Fort Rocky lagoon and 16.5 ‰ at Station B. A value of 4.6 ‰ was obtained inshore to the east of the mangroves near Palisadoes.

Only limited observations were made on the enormous mortality following this rain; the following gives an outline of the situation:

Station A

On 8th October (Salinity 25.4 ‰) there was no apparent mortality. Among animals found alive were various hydroids, *Telesto* sp., *Phyllactis flosculifera*, an unidentified colonial actinian, *Lytechinus variegatus* and *Ascidia nigra*. By 18th October almost all of these were dead except for some hydroids and a little *Telesto*.

Station B

On 8th October (Salinity 16.5 ‰) hydroids, ascidians, ophiuroids, holothurians and some *Echinaster echinophorus* were all dead. Among a big patch of sabellids about 50% were still alive. By 18th October (23 ‰) everything in the channel was dead except for a few fishes and crabs which may have re-entered from deeper water as the salinity rose again.

Fort Rocky Lagoon

This was only examined briefly on 8th October when it was clear that many animals were dead. By 18th October there was barely a living thing remaining on the mangrove roots and the water in the lagoon had become fouled by decaying matter. Around the 30 cm level from the surface a few oysters (*Isognomon alatus*) and a small

lamellibranch (*Brachidontes exustus*) were still alive and at 1 metre a purple sponge appeared to be alive. Otherwise an extensive search revealed no living animals.

Station C

At this time a raft at Port Royal had communities of *Ascidia nigra* on panels at 2 levels, one set between 1.3 metres and 1.7 metres below the surface, the other between 2.2 metres and 2.6 metres. These panels were examined on 3rd October and again on 27th. During this interval 87% (154 out of 179) of the population at the upper level had died and 33.5% (45 out of 145) at the lower level had died. (Further details of this will be published in a later paper on the ecology of *A. nigra*.)

RECOVERY OF NORMAL SALINITY

Normal salinity in the harbor and lagoons is about 35 ‰. Examination of Table V shows that in Fort Rocky lagoon the salinity was 32.8 ‰ in early December 1958 and had reached 34.5 ‰ a month later so that a period of 2 to 3 months was required for recovery. In the main harbor east of the entrance to Hunt's Bay salinities of over 34 ‰ were reached by 10th December and by 15th January were generally slightly over 35 ‰.

RECOLONIZATION

Following the October 1958 rains the mangrove area was examined on 6th November, 9th December and 9th January. In November the roots were quite bare except for a few lamellibranchs, notably *Isognomon alatus* and *Brachidontes exustus* well below the surface, and 2 small ascidian colonies 0.75 metres below the surface (*Ecteinascidia turbinata* and *Perophora bermudensis*). By December limited colonization had occurred particularly of sponges, serpulid worms, a few sabellids, numerous balanoids and the two lamellibranchs cited above. Several species of ascidian had recolonized, notably *Ascidia nigra*, *Symplegma viride*, *Diplosoma macdonaldi* and the two species already mentioned. Actinians were notably absent at this stage. By January there had been considerable development of this community and hydroids, actinians, the lamellibranch *Crassostrea rhizophorae* and the ascidian *Botryllus planus* had also recolonized.

CONCLUSIONS

Kingston Harbor is a partially land-locked salt water lagoon with a normal salinity of about 35 ‰ and supporting a flourishing marine fauna and flora. In some years heavy rainfalls in spring

or autumn may result in flooding of the harbor and its lagoons with fresh water; this enters as river flow, as drainage from the mangrove swamps and as direct rainfall on the surface. It spreads out over the surface as a brackish water layer particularly at the western end of the harbor. Return to normal salinity in certain places may take from 2 to 3 months.

The biological effects of these floods are disastrous and result in the almost total destruction of marine sedentary animals in the affected zone. The primary cause of death in the community is almost certainly the rapid reduction in salinity but other associated factors may contribute subsequently. In particular the fouling of the water by decaying animals in Fort Rocky lagoon suggests that in such enclosed lagoons deoxygenation, and possibly disease, may follow and further enhance the mortality caused by lowered salinity. Temperature shock is unlikely to be important as a cause of mortality. Table VI shows the sea surface temperatures at Port Royal in the first 10 days of October, 1958. Temperatures fell from 30.2° C on 2nd October to 26.0° C on 7th, a total drop of 4.2° C but spread over such a long period that by itself it would be unimportant as a mortality factor. No records are available for 4th and 5th and the drop of 1.8° C between 3rd and 6th is the greatest single drop recorded in the Table. A drop of 2.2° C was recorded between 3rd and 4th September without any noticeable mortality occurring; it seems reasonable to suppose therefore that a drop of 1.8° C would not produce temperature shock even if it had occurred in one day. The lowest temperature recorded in this table (26.0° C) is reached in January under normal conditions in Kingston Harbor. In May 1958 temperatures fell 2.8° C between 17th and 20th but there are no records for the intervening dates to show how fast this occurred. In October 1956 temperature fell by only 1° C.

TABLE VI. Sea surface temperatures at Port Royal in the first 10 days of October 1958
(Reproduced by permission of the Director, Survey Department, Jamaica)

Date	1	2	3	4	5	6	7	8	9	10
Temp. °C.	30.2	30.2	29.0	—	—	27.2	26.0	27.2	26.2	26.8

The situation here differs from that described for Lagos lagoon by Hill and Webb (1958) in that it is irregular and unpredictable and only affects the surface layers; it depends on exceptional rainfall over a period of a few days. In Lagos the flushing of the lagoon is a regularly

occurring annual phenomenon affecting all levels and some animals *e.g.* *Branchiostoma* (Webb 1958) have developed special adaptations in connection with it.

Following the mortality in Kingston Harbor large areas of settlement surface are made available for recolonization. Many sedentary forms, notably cirripedes, serpulids, and ascidians breed throughout the year (Goodbody *in press*) and recolonization begins as soon as conditions are again favorable. The parent stock for this recolonization must be situated in the deeper layers of the harbor and its lagoons which remain unaffected by the flood waters. This situation is again in contrast to Lagos where recolonization is effected from populations outside the harbor and away from the influence of freshwater flooding (Sandison and Hill 1959).

One interesting feature of this situation is that the mangrove root communities of the lagoons in Kingston Harbor may seldom reach a climax condition due to repeated destruction of developing communities.

One further point of interest was observed at Port Royal in 1958. For many weeks after the rains the water at Station C was green and cloudy in the early morning but by mid-day had usually become blue and clear like open ocean water. Salinity determinations showed that the green water was of low salinity (24 to 27 ‰) while the blue water was usually of high salinity (34 ‰) (Tables IV and V). This phenomenon is almost certainly related to the development of sea breezes in the daytime which probably push a tongue of ocean water through the harbor entrance past Port Royal. This must recede again at night and allow the brackish water to return. Sessile animals living near the surface here and which survive the initial killing must thus be subjected to repeated and rapid salinity changes for several weeks.

SUMMARY

Three mass mortalities of sedentary animals have been studied in Kingston Harbor, Jamaica.

The first one occurred in October 1956, the others in May and October 1958.

On each occasion the death of animals followed immediately on unusually heavy rains. Rainfall data for the 4 years 1956-1959 show that they coincided with the only occasions on which more than 300 mm of rain fell in a month and more than 100 mm in a single 24 hour period (Table I).

Following these rains surface salinities in the harbor fell rapidly from a normal value of 35 ‰ to less than 20 ‰ and sometimes as low as 5 ‰. Death is probably primarily caused by the low salinity but disease and de-oxygenation may later play a part in some places.

Return to normal salinity may take 2 to 3 months and recolonization has started within 2 months.

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REPORTS

DIURNAL VARIATIONS IN CHLOROPHYLL *a* CONTENT OF SOME FRESH-WATER ALGAE

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INTRODUCTION

Diurnal variations in the rate of photosynthesis of phytoplankton of natural waters have been recently described. Doty and Oguri (1957) observed variations up to eight-fold in the ability of oceanic phytoplankton to photosynthetically fix carbon. The high values occurred during evening hours. The authors suggest the possibility of variations in chlorophyll content as an explanation of the fluctuation in productivity. A similar periodicity in photosynthetic activity, but of smaller magnitude (only two-fold), was observed by Yentsch and Ryther (1957). They found a daily periodic variation in chlorophyll content and rate of chlorophyll synthesis. Shimada (1958) likewise found diurnal variation in photosynthesis rate correlated with a similar variation in chlorophyll *a* concentration of phytoplankton.

These observations were done on natural oceanic phytoplankton populations. To further study the concept of a daily variation in chlorophyll concentration, we attempted to measure the chlorophyll content of several unicellular algae grown under laboratory conditions during a 24 hr period.

METHODS AND RESULTS

Pure cultures of *Chlorella* sp., *Stichococcus* sp., and *Ankistrodesmus* sp., isolated from lakes on Afognak Island, Alaska, and *Euglena gracilis* strain Z, obtained from Dr. L. Provasoli of the Haskins Laboratories in New York, were studied. Culture media for the first 3 species consisted of autoclaved natural creek water enriched to contain 100 mg% KNO₃, 10 mg% KH₂PO₄, 10 mg% MgSO₄, 4 mg% CaCl₂, 0.3 mg% FeCl₂, and 2 ml soil extract per liter. *Euglena* was cultured in a medium as above but further enriched to contain 400 mg% Bacto-tryptone, 10 mg% yeast extract, and 1.5% sucrose. The cultures were grown in pyrex flasks without agitation on a table top illuminated from above by a battery of daylight fluorescent tubes. Light intensity at the table top level was about 250 ft-c. Room temperature during the experimental period was from 15°-25° C. The cultures were illuminated for 12 hr (9 AM to 9 PM) and were in the dark for 12 hr (9 PM to 9 AM), except when otherwise indicated. After at least 7 days of growth under these conditions, appropriate samples were withdrawn from the flasks at regular intervals, usually every 2 hr. The flasks were well shaken to insure homogeneous samples. The cells were harvested on millipore membrane filters. Pigments were extracted and chlorophyll *a* concentrations determined by the method of Creitz and Richards (1955). A Beckman model DU spectrophotometer was used for the determinations.

The results of an experiment on *Ankistrodesmus* sp. are charted in Figure 1A. No difference is apparent in the chlorophyll content of the culture during the 24 hr period. Curve 1B depicts the results of an experiment on *Chlorella* sp.; again no obvious variations are apparent. In Figure 1C the results of 3 experiments on *Stichococcus*

sp. are graphed. Results of two separate experiments on cultures maintained on a light-dark schedule (Fig. 1C, curves a and b) and one experiment on a culture maintained under continuous illumination (Fig. 1C, curve c) are shown. The chlorophyll level of the culture maintained under continuous illumination did not vary during the experimental period. The cultures maintained under a light-dark regime show considerable variation. The high and low values for the 24 hr period did not coincide in the two experiments; however the order of magnitude of the variation was similar.

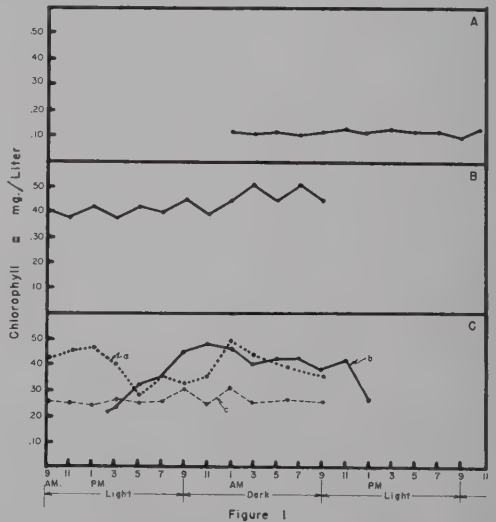


FIG. 1. Chlorophyll *a* concentration in (A) *Ankistrodesmus* sp., (B) *Chlorella* sp., (C) *Stichococcus* sp. during a 24 hr period. C (a) and C (b) represent 2 independent experiments performed under a light-dark regime during Dec., 1958, and Jan., 1959, respectively. C (c) was maintained under continuous illumination; the experiment was performed in Dec., 1958, in conjunction with C (c).

Results of two experiments on *Euglena gracilis* are charted in Figure 2. The first experiment (line a) was conducted for 24 hr. The second experiment (line b) was extended to over 60 hr with sampling every 3 hr. The drop in the level of chlorophyll seems to be correlated with the onset of the dark period. However, the beginning of resynthesis of chlorophyll appears prior to exposure to light.

Of the 4 freshwater unicellular green algae studied, 2 (*Stichococcus* sp. and *Euglena gracilis*) show considerable daily fluctuation in their chlorophyll *a* content. The

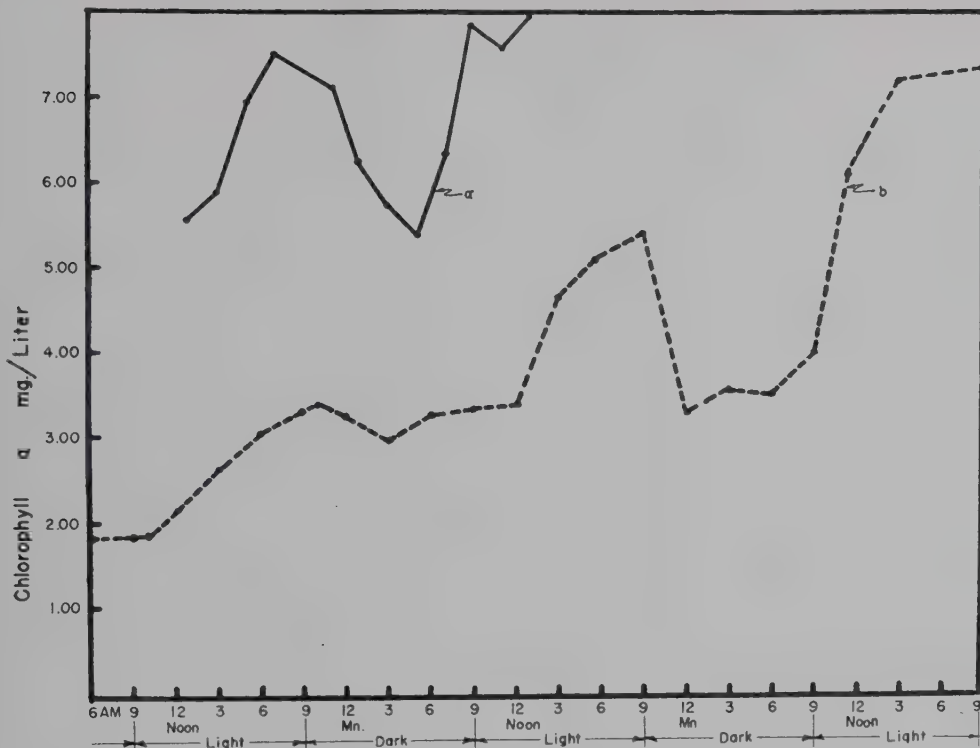


Figure 2

FIG. 2. Diurnal changes in chlorophyll *a* concentration in *Euglena gracilis*. A and B represent 2 independent experiments, performed in Dec., 1958, and Jan., 1959, respectively.

order of magnitude of the difference in chlorophyll *a* levels between the high and low points during a day is similar to the observed variation in natural marine planktonic populations described by Yentsch and Ryther (1957) and Shimada (1958). Variation in light intensity as a causative agent for the fluctuation in chlorophyll level can probably be ruled out. Though the light intensity on the table top was not constant, variations in intensity were not large. The table was at a back wall of the laboratory and the experiments were performed during Dec. and Jan., during which time the few daylight hours are usually overcast in Juneau.

Since absolute controls of physical conditions such as temperature were not possible, it was not feasible to design a more sophisticated experiment for the determination of factors affecting the variations in the rhythm-time for this phenomenon.

The experimental results corroborate the reported observations on the existence of appreciable diurnal variations in chlorophyll content in at least some, but not all, planktonic algae. This work also indicates that

daily fluctuations in chlorophyll *a* content are not unique to oceanic plankton but occur in freshwater algae as well.

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NATURAL SELECTION AS AN ECOLOGICAL CONCEPT

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In 1959 the centennial of the publication of Charles Darwin's *Origin of Species* was celebrated throughout the world by those interested in evolutionary theory. In 1958 at the zoological congress in London a special session marked the centenary of the presentation to the Linnean Society of the doctrine of natural selection by Darwin and Wallace. During these two years numerous writers have reviewed the history of the concept of natural selection and its relation to evolutionary theory. With the notable exception of Stauffer (1959), few have alluded to its relation to ecology. It is likewise apparent that many ecologists have not seen the direct relations of natural selection to their investigations. This is not surprising, however, because Darwin presented his theory as an evolutionary explanation of the origin of species, and much of this explanation became incorporated into it. So much confusion surrounds our conceptions of species, evolution and natural selection that the relation of the latter to ecology has never been wholly clear. In emphasizing both the problem of the origin of variation and the consequences of natural selection, the nature of the elemental biological operation of selection has not been explicitly expressed. The operational level of this event became obscured and thereby its important relation to ecology likewise was obscured. Recognition that natural selection takes place at the level of the relation of the individual organism and its environmental conditions places it by definition in the realm of ecology.

A survey of the literature of natural selection also displays an undercurrent of perplexed and subtle dissatisfaction with the concept. It is implied that either more thought or further investigation is needed to discover the full significance of natural selection. We think that some of this dissatisfaction may evaporate when it is pointed out that many confusions stem from problems in expressing and organizing knowledge rather than from the facts pertaining to organisms. Biology is a body of knowledge about organisms and as such must satisfy not only the laws of nature but the laws of knowledge (Mason and Langenheim 1957). Therefore semantic analyses of the concept of natural selection were made according to the principles of the Theory of Signs (Morris 1938). As a result of this examination and the clarification that follows, the concept of natural selection emerges not only in a more simple and orderly role in evolutionary theory, but also as one of the basic unifying concepts of biology.

It is a pleasure to acknowledge the stimulating criticism of the manuscript by many friends and students, especially Dr. Edwin Tisdale, Dr. R. L. Langenheim, Dr. Helen Sharsmith, Annetta Carter, Jack Wolfe, V. A. Zullo, Stanton Cook and S. G. Smith.

METHOD OF LANGUAGE ANALYSIS

It is our purpose to demonstrate the distinction between a concept of natural selection based upon an analysis of confirmable experience, and the many conceptions of it in the history of usage of the term. Perhaps it is important to point out that a distinction is drawn between "concept" and "conception" (Langer 1953). Langer's distinction is that a concept rests upon confirmable experience such that it can be rigorously defined within the limits of our knowledge. A conception, on the other hand, may be our personal understanding or misunderstanding of the concept. More often, in the absence of the defined concept, a conception is the understanding of the whole context of

loosely aggregated facts and their relations. It may thus include extraneous complexities or be incomplete. Sometimes it is an incommunicable mental picture which stands as the symbol of the concept. It appears that most authors' conceptions of natural selection have given them so complete a feeling of comprehension that they have thought further clarification in terms of rigorous definition unnecessary. The diversity of conceptions, however, indicates a need for evaluation of the basis of the concept.

The semanticist tells us that meaning is a property of statements; therefore to establish the meaning of any term one must place it, as a symbol of a concept, in statement form. The specific statement form for an analysis is "x is is true if and only if the following is true." There follows an enumeration of the necessary and sufficient truth conditions that establish the truth value of x. Truth, like meaning, then, is also a property of statements. The meaning of the statement is determined through the establishment of the necessary and sufficient truth conditions upon which the statement rests. Rynin (1952) calls attention to the nature of the test for meaning and points out that it does not consist of introspection or merely seeking a feeling of comprehension. Rather, meaning in the last analysis must be thought of as replacement of symbols in statements by events or experiences which are their meanings. These "replacements" provide the conditions whereby the statement may be said to be true or false. Hence they are its truth conditions and constitute the basis of the concept.

A necessary truth condition is one whose absence renders the statement false. Sufficient truth conditions are those which, when all present, render the statement true. Thus a necessary truth condition may be present but alone does not establish the whole truth. Only sufficient truth conditions establish the truth of the statement. The substitution of truth conditions determined for the symbol "x" in the statement form above would make the symbol "x" synonymous with the term to be defined. We thus would have the necessary 1:1 relation between the term and its definition.

ANALYSIS OF DARWIN'S CONCEPTION OF NATURAL SELECTION

If we turn to the history of the conceptions of natural selection we will see that the traditional views have grown out of the conceptions of various workers. First, it is important to recognize that this history has been inextricably connected with that of our knowledge of evolution. According to Jepson (1949) natural selection was described as related to adaptation as early as 400 BC by Empedocles. However, the principle did not receive impetus until Darwin and Wallace suggested that evolution was controlled by the mechanism of natural selection. Although both Darwin and Wallace (1859) presented the same principle, they emphasized different points in its presentation. With due respect to the contributions of Wallace (1870, 1889), our analyses shall be restricted to Darwin.

Unfortunately Darwin, in his eagerness to set forth natural selection as an explanation of the origin of species, employed language that inadvertently caused his readers to incorporate much of this explanation into their conceptions of natural selection. By failing to clearly define natural selection and by discussing it in terms of

its consequences, Darwin's language is often ambiguous as to what constitutes the process of selection and its distinction from the explanation of evolution. However, the most fundamental contribution of a man of genius may not always rest wholly in what he *says* of a subject. Basic ideas resulting from observations from which he deduced incomplete and unclearly expressed statements may be more important. Thus it behooves us to seek out and try to understand these original perceptions in the hope that we may grasp the fundamental ideas and conceptions that they generated in his mind. Often there is concealed information and clarity that may make his discourse serve more effectively the useful purpose he foresaw for it.

To get at the facts necessary to our analysis of Darwin's conception of natural selection, the *Origin of Species* (Darwin 1869) was searched for a specific definition. Instead of a definition we were confronted with a wealth of examples of the consequences of natural selection each in turn presented by the author with the expressed hope that it would make clear what he meant by the term. He speaks of it as a principle but does not enumerate either its properties or any details of it as an elemental operation.

Several statements regarding the fundamental ideas of natural selection appear to be as close to a definition as Darwin comes. The following quotations seemed most significant to us: "I have called the principle by which each slight variation, if useful, is preserved, by the term natural selection. But the expression often used by Mr. Herbert Spencer of the survival of the fittest is the more accurate and sometimes equally convenient" (p. 52), and "The preservation of favorable individual differences and variations, and the destruction of those which are injurious, I have called natural selection or the survival of the fittest. Variation neither useful nor injurious would not be affected by natural selection" (p. 64).

It is important to note that in the first statement, by referring to natural selection as a principle having certain consequences and, in the second, as an act of preservation with preserving consequences, Darwin drew a distinction between natural selection and its consequences. By expressing it in this way, natural selection is presented in the sense of an undefined primitive notion which Darwin referred to here as a principle and elsewhere as a "blind force operating in nature." It is this distinction between natural selection and its consequences that gave to the theory the logical power adequate to the impact it has had on biology. This is important because in some subsequent statements by Darwin and those of his successors this distinction has not always been kept clear, thus leading to ambiguous language.

As we review these quotations from Darwin and set his facts in the context of a formal statement for analysis we have: x is natural selection is true if and only if:

1. It is a principle whereby
 - a) "useful variations or favorable individual differences are preserved"
 - b) "injurious variations are destroyed"
 - c) "variations neither useful nor injurious are not affected."
2. The fittest survive.

Obviously this is not a definition which describes and sets forth the properties of the elemental operation of natural selection. It is an introduction to a conception via its consequences. Each of these statements asserts a consequence of natural selection which, obviously, is something other than the process. The first alludes to a step in evolution. The second refers to rejection. The

third sets forth circumstances by which nothing happens and the fourth is survival.

If it is assumed, as many do, that these statements represent the truth conditions significant to Darwin's conception of natural selection, certain problems are raised. The result of Darwin's detailing consequences of natural selection has led to ambiguous language that rarely follows such a method of presentation. This is because the more significant evolutionary consequences of natural selection, as expressed by both Darwin and by later evolutionists, entail a sorting of properties through variation in reproductive sequence, a sorting of genes in reproductive sequence, and a sorting of gene frequencies in successive states of populations. This abstracted evolutionary sorting is selection-like and operation-like; hence the term "selection" has been applied to it. It is not surprising that in the minds of many, therefore, the description of these abstract sortings is considered a description of the process of natural selection. The term "natural selection" not only came to symbolize these 3 abstract notions of selection, but, in order to account for survival, included the implied selection of individuals by their environments. When viewed in terms of sets of identical truth conditions, "natural selection" and "evolution" thereby have become synonymous in usage. The distinction between the selective principle and its consequences has become lost. Furthermore, the inclusion in a single concept of environmental selection and these selection-like abstractions from different levels of abstraction violates the theory of types and is logically inadmissible. To state that natural selection so defined gives rise to evolution is to state tautologically that evolution follows from evolution. The conclusion merely reiterates the premise, and natural selection cannot serve the role envisaged for it by Darwin.

Let us look further into what happens to our language when such abstract consequences are regarded as the source of meaning of "natural selection." When we employ such words as "variation" and "difference" we are talking about a relation between unlike individuals. Emphasis is placed upon such properties of organisms whereby individuals differ from one another. By focusing our attention on properties that vary, our language is led to circumvent individuals and properties that do not vary. These appear to be left hanging in a conceptual vacuum in the nebulous realm of the "not affected." Since selection implies its complement "rejection" (or not selected), the implication is clear that these are rejected. Yet they survive. When useful properties are considered as essential to selection, implication indicates that because these surviving individuals were not selected their properties must be useless. Obviously no one means this. It is strictly a case of logical implication playing a trick on us through our imperfect language.

Still another difficulty arises because it is not wholly clear just what is being selected. Is it *individuals* with useful variations? Or is it "useful" varying *properties* taken out of a context of other "useless" and non-varying properties and intellectually isolated as a single object of thought? To speak thus on the level of properties demands abstraction by human observers. Such abstraction obscures both the locus and the nature of the elemental selective operation. Is natural selection a relation between an individual organism and its environmental condition? Does it occur in meiosis? Is it an influence of genic materials on ontogeny to change properties? Is it a genetic operation in populations such that successions of gene frequency may be spoken of? If it is an elemental operation, it must be one and only one such operation. Any combination must of necessity involve abstraction

into an operation-like concept. If it is one and only one elemental operation, it must be such conceptually that all others significant to evolution may be deduced from it in a manner consistent with the laws of the organization of knowledge and without violating the laws of nature. Thus we have been led, by the implications of our statements, into confusing the *description of evolution with its explanation*.

It should be clear that Darwin's conception of natural selection involves the selective relation of an organism with its environment. In this respect Darwin was closer to the ecological implications of natural selection than most of his successors. However, by treating his subject from the point of view of the consequences of natural selection in the origin of species without clearly defining its operation, the way was left open to all of the confusing views that have entered subsequent conceptions of natural selection.

ANALYSIS OF THE CONCEPTIONS OF NATURAL SELECTION OF THE POPULATION GENETICISTS

The history of the theory of natural selection subsequent to Darwin has been basically a continuation and amplification of similar ambiguities of language. Criticism was directed toward the role of the theory in evolution and its exemplification rather than toward the meaning of the concept. Therefore basic confusions have persisted. The strongest opposition to the theory came from the mutationists who were seeking in it evidence of the origin of variation. They pointed out that natural selection did not account for the origin of variation and therefore was inadequate to explain evolution. As a result of the discovery by de Vries and Johannsen of variability produced from mutations, the theory of natural selection was temporarily replaced by the mutation theory. This conflict arose from a confusion between the operation of natural selection with the origin of what is to be selected. It resulted in further confusing natural selection with evolution which is a sequence of selective operations involving change. With the advent of population genetics, it became clear that other cytogenetic forces also produce change. These, together with mutation and other mutagenic forces, were incorporated into the neo-Darwinian theory of natural selection as its creative or diversifying element. It is significant to point out that incorporation of the origin of variations into the concept of natural selection was still clung to; the ways in which it was accomplished, however, were broadened. It is probable that this preoccupation with the origin of variation as an explanation of evolution has resulted in natural selection being primarily the concern of the geneticist rather than the ecologist.

Contributions of the population geneticists to the general subject of selection are so voluminous as to preclude review of the entire literature. Therefore, precise semantic analyses have been made of the conceptions of natural selection of only a few of the modern population geneticists and evolutionists (Morgan 1903, Fisher 1930, Haldane 1936, Dobzhansky 1941, Nash 1944, Lull 1947, Holmes 1948, Muller 1949, Jepsen 1949, Wright 1949, Stebbins 1950, Simpson 1953, Simpson, Pittendrigh, and Tiffany 1957, Lerner 1958, Sheppard 1958). In the interest of brevity and to avoid repetition, only a summary of the results of our analyses with pertinent examples is presented.

Despite considerable confusing diversity in details of the conceptions of natural selection expressed by the modern geneticist and evolutionist, several basic and unifying ideas emerge from these analyses. First, these workers are concerned with various mechanisms whereby

variation is produced. Second, they express the variation of properties in terms of gene action. Third, the assessment of gene variation is made within a population, thus leading to the prominence of such concepts as gene frequency. Fourth, to insure the continuation of evolution, they demand reproductive continuity as a part of selection. Fifth, most of them indicate that useful variations are cumulative through the action of natural selection. Sixth, they consider rejection as operationally significant to the concept "selection."

The problem of the restriction of the concept of natural selection to just those properties which vary has been discussed in connection with Darwin's conception of natural selection. It is understandable how, in their preoccupation with properties that vary, subsequent thinkers inadvertently abstracted these sequences of variable properties from their operational context as a single object of thought. In this abstracted state the sequence of properties stood more clearly in their relation to evolution. We must repeat that it is not surprising, therefore, that they should have regarded this abstracted sequence and the cytogenetic operations responsible for the sequence as the process of natural selection. It must be reemphasized that this abstraction by humans is entirely apart from the empirical biological operation of selection. From this abstraction a concept emerges that is operation-*i.e.* This has been confused with the actual operation in which only those physiologically constituted to function in the available environment are selected for survival from a given set of differing individual organisms. The results of any cytogenetic events that produce favorable variations are thereby in turn selected. The abstractions that go beyond this, to unify or to interpret and to explain the origin of variation in its relation to evolution, involve classification.

Although the inclusion of the origin of variation prevailed among most workers, Dobzhansky (1941), for example, realized the difficulties of its incorporation in the concept natural selection. He states, "... the origin of variation is a problem entirely separate from the action of selection. The theory of natural selection is concerned with the fate of variations already present ..."

Holmes (1948), however, questions the assumption that variation should be regarded as something given in nature upon which natural selection acts. This seems to him to imply that variation itself is not a product of natural selection. The ambiguity is apparent in his discussions of gametes. He seems to regard these as involved in a continuity of the selective process from gamete formation through the formation of the zygote. Actually, gamete formation is under the influence of a selective operation on the parents. In addition, selection operates on the gametes themselves during any independent existence; the formation of the zygote initiates a new selective regime.

It has been pointed out that by including the description of evolution in the conception of natural selection, a confusion of levels of abstraction is generated. The neo-Darwinians, not having analyzed the sources of ambiguity in Darwin's language, were led into further levels of abstraction when they spoke of natural selection in terms of the sorting of genes through the reproductive sequence. For to discuss natural selection at the level of gene operations in reproductive sequence is to add another level in order to account for the ontogenetic origin of properties. Although genes are themselves properties, because their role is to direct the organization of other properties in ontogeny, the level of organization in knowledge is different. Therefore, they, in their role in ontogeny, must be treated on a different logical level. It follows that the

sorting of genes must be handled in our language as logically different from the sorting of their resulting properties. By regarding these sortings as the process of selection, this gives a third conception of the term "natural selection" as employed by the neo-Darwinians. The conceptions of natural selection now include: 1) selective relation between an organism and its environmental conditions, 2) selection of properties in reproductive sequence, and 3) the sorting of genes. The first is an empirical relation whereas the latter two each are abstracted from a different and separate set of facts taken from a succession of environmental selections.

The emphasis on gene sorting requires the interbreeding population as the locus of operation. However, no elemental biological operation takes place *above* the level of an individual organism. An adjustment in understanding that yielded a feeling of comprehension was achieved by adopting the statistical concept of "gene frequencies." There is herein an assumption of an interpretation in terms of an elemental biological operation significant to natural selection. We have thus a fourth notion of selection at an even higher level of abstraction. This emphasis upon gene frequencies also has led to some misunderstanding regarding the role of the concept population. "Population" has been reified to the extent that some workers discuss selection as involving the "physiology of the population not of individuals" (Stebbins 1950). It should be emphasized that as instruments of knowledge, gene frequencies and other population phenomena result from classification of empirical knowledge pertaining to individuals.

Many workers have stated that the purpose of survival is reproduction. This point is well exemplified in the definition of natural selection presented by Simpson, Pittendrigh, and Tiffany (1957). They state, "The process of natural selection, which is the sum total of life's hazards, selects on the basis of competence to live, or rather competence to reproduce." They compare natural selection to a game wherein the objective of each individual is reproduction. Through the reproductive sequence an evolutionary advantage is accumulated by the more fecund, and success becomes a matter of chance favored by large numbers. Whereas they speak of selection resting in a "competence to live," their qualifying phrase indicates that this is of little consequence against the statistical chances of survival arising out of fecundity. What is accomplished by conceptions such as those of Simpson, Pittendrigh, and Tiffany is the notion of reproductive continuity necessary as a context for evolution. They are discussing evolution and not natural selection. An individual that fails to reproduce is as effectively selected as one that does reproduce. What the former fails to accomplish is an effective role in any further evolution of the population.

Darwin's notion that useful variations are selected and harmful variations are rejected has lead directly to the modern evolutionist's conceptions of adaptations and the accumulation of adaptations as an evolutionary consequence of such selections. This idea has been so significant that a large terminology, such as "adaptive response," "adaptive radiation," etc. has developed to express its various features.

Significant ambiguity results from two very different conceptions of adaptation. One conception is contained within the other. The range of physiological capacity of the organism, or any of the elements of this range, may be spoken of as an inherited adaptation. Some distinguish this as "preadaptation." Within this range of preadaptations some individuals effectively adjust and are said to be currently "able to adapt themselves to different en-

vironmental conditions." The one is an inherited natural state for each particular organism; the other is an operation or physiological adjustment by the organisms within the limits of their inherited physiological capacity. It follows that the word "adaptation" is apt to mean significantly different things to different people. This may account for the differences in the manner in which the terms "variation" *per se* and "adaptation" are handled in the literature. Dobzhansky (1941) maintains, and we think correctly, that adaptation is the concern of natural selection whereas variation is the concern of evolution. However, when we shift to a context of reproductive continuity and discuss the cumulative nature of adaptiveness ("adaptations" in the current literature) we are discussing variation in adaptiveness in reproductive sequence. Our subject then shifts from natural selection to evolution. Thus the class of things that varies comprises two subclasses, namely, those that vary adaptively, and those that vary otherwise. To discuss variation in reproductive sequence, regardless of which subclass is our subject, is to discuss evolution.

Finally, most modern population geneticists and evolutionists discuss rejection as though it played a continuing active role in the selective operation. They discuss a population whose members operate strictly within the genetic influence of what is there and the evolutionary consequences of this. Their language implies that those organisms rejected, and hence not there, somehow continue to influence the result by not entering into it. Implications of this problem will be discussed later. However Simpson, Pittendrigh, and Tiffany (1957) provide a slightly different approach in the definition quoted above. Here it appears that "life's hazards" are the selecting agents rather than favorable media of the environment that permit survival. This anthropomorphic notion of the "struggle for existence" apparently has so thoroughly permeated the language of natural selection that it is often assumed to be a part of it. It is a formal analogy that belongs to the explanation of the role of natural selection in evolution rather than to an understanding of the process of natural selection.

In summary it appears that in the current conceptions of natural selection there is confusion of the elemental biological operation with the evolutionary sequences that are explained by means of natural selection. This explanation seems to demand a level of abstraction in which the sequential change from generation to generation can be isolated as single objects of thought. Such an intellectual operation is valuable, but sometimes the patterns of property sorting, of gene sorting, of gene frequencies and their consequences observed through generations are mistaken for the elemental biological process of natural selection. Natural selection cannot be described as an elemental biological operation at the abstract level of evolution. It occurs at a level of separate and discrete acts which together in ordered sequence constitute a group whose properties may be abstracted to the evolutionary level. The result of confusion in these matters is that we think we are discussing natural selection when truth conditions that give meaning to our statements indicate that we are actually discussing evolution.

ANALYSIS OF THE CONCEPT NATURAL SELECTION

With the previously discussed confusions in mind we may now seek to establish the truth conditions upon which a rigorous concept of natural selection may rest. The following statement seems to us to clarify the problem.

"X" is the process natural selection is true if and only if:

1. It comprises elemental operational relations between an individual organism and its environmental conditions such that the organism satisfies all of its physical needs for establishment and survival.

2. It endures through the ontogeny of all stages of the life cycle to successor organisms in reproductive sequence, if there are any.

The first statement is necessary because it accounts for the physical basis for survival in terms of the operations of the organism as conditioned by environmental conditions. It is insufficient only if it is successfully argued that the term "organism" does not imply its ontogeny and the separate and independent stages of the life cycle. In that event the second statement is necessary especially to include any independent environmental relations in the alternation of generations as well as those of gametes, spores, and seeds, etc. Although successor organisms are essential to evolution, it is important to note they are not essential to the process of selection of any predecessor generation.

To demonstrate the sufficiency of these two statements, we will attempt to show that all of the facts necessary to an understanding of the role of natural selection in biology are either asserted or implied. The sufficiency resulting from implication stems from the fact that the *operational* relations of the organism to its environment are physiological. An understanding of this makes clear that there are inherited limitations in tolerance which are meaningful in terms of definite ranges of environmental conditions. There is thus implicit in our definition the idea that the organism arrives in the habitat already endowed through prior genetic activity with its physiological capacity as a prior adaptation. This is a fact in the history of the conditioning of the organism and, although pertinent to the origin and selection of this organism, it is not a part of the selective act upon this organism. The further operations of meiosis and mitosis and any attendant mutagenic events within the selected organism do occur under the influence of this act of selection. They in turn are part of the history of the next discrete and independent descendant unit of selective operations.

It is also essential to understand that natural selection permits each like as well as unlike organism to live and carry on all of its vital processes. Therefore every ontogenetic event of physiology and morphology that is in relation to environmental conditions is a part of the selective operation. This includes any independent stages of the life cycle necessary to the generation of the next selective step. Natural selection is not restricted to just those processes that may introduce change into a population. Hence, organisms reproducing asexually and those that may not reproduce at all are not precluded.

"Rejection," which Darwin made a part of his statement and subsequently has been considered necessary to natural selection need not be included in our definition. This concept provides subtle semantic and logical problems which require careful and detailed attention to clarify. All propagules presented to their environment together comprise a class. Selection provides the basis for a subclass of selected organisms and its complement, which is the subclass of rejected organisms. The class selected organisms implies that others have been rejected, but it must not be supposed that selection and rejection are thereby either the same or a similar operation. The term "natural selection" is concerned only with the selective operation and the selected organisms. The circumstances of the selection of an organism are the sources of the truth conditions which will confirm natural selection. From knowledge of fecundity of organisms and of the

number of propagules produced, compared with the number of survivors, an inexact comprehension is gained of the rejected. Whereas it is known that there are rejected organisms, except in experiments it is often difficult to point them out to confirm our statements.

The subject of rejection in its formal nature is much like the subject of isolation in the literature of genetics. On an operational level the population that survives or that which is isolated, is permitted to operate strictly within the genetic influence of what is selected or what is isolated. The individuals of these selected and isolated populations provide the only material for operations significant to our subjects. This says nothing about rejection or the rejected organisms themselves or about those isolated against. In both subjects there is an inherent human tendency to discuss the negative aspects, as though the individuals rejected or those isolated against continued to influence *actively* the result by not being there.

However, the notion of rejection can be abstracted from its context of noninfluence and be employed to amplify the *explanation* of the restrictive nature of the influences present and to explain the sorting accomplished. The role of rejection in discourse is thus explanation of the completed and classified results of natural selection rather than description of its continuing operation. Rejection in each individual case eliminates the individual from any operation of natural selection in that case. Our subject must be discussed with the awareness of the distinction between natural selection as an elemental biological operation and the abstractions, explanations, and inferences from a sequence of selections that humans build into evolutionary ideas. It is only in these explanations that the role of rejection, in an abstract sense, can take form in a positive statement bearing on evolution.

To some the absence of a statement involving indirect influences on selection may cause concern. Such properties of organisms as protective coloration and other protective structures do influence natural selection by inhibiting rejection. This inhibition of rejection may occur at any stage in the life cycle. Actually these indirect influences are implied in the first statement because when effective, the organism is permitted to continue to satisfy its physical needs for survival.

The above analysis sets forth only the strictly biologically operational relations between the individual organism and its environmental conditions. In setting forth the unity of each operation cognizance is not taken of any other organism, whether like or unlike. The selective operation on each organism is thus construed as a logically self-contained set of facts. When an understanding of the results of natural selection is sought, we move from the data presented by any given case to that of many given cases, both as of any given time and through any sequence of generations through time. Our problems then shift from perception of facts to classification of our conceptual knowledge and the inferences and deductions that may be derived therefrom.

Figure 1 graphically presents examples of the organization of knowledge about natural selection. In the left hand column are indicated the empirical sources of knowledge, namely, each individual organism separately and independently in selective relation with the elements of its environment. It should be reemphasized that it is in this *empirical relation of each organism to its environmental conditions* that all of the facts pertinent to natural selection take place. All else that has been traditionally associated with this term results from classification and deduction.

Because we are interested in the role of natural selection as it may be interpreted in terms of species popula-

Fig. 1. CLASSIFICATION (ORGANIZATION OF KNOWLEDGE)

SOURCES OF KNOWLEDGE

Data from many individuals

SELECTIVE OPERATION ON EACH INDIVIDUAL ORGANISM SEPARATELY AND INDEPENDENTLY IN SELECTIVE RELATION WITH THE ELEMENTS OF ITS ENVIRONMENT

CLASSES (POINTS OF VIEW)

Class Level 1

CONTEMPORARY SELECTIONS

SEQUENTIAL SELECTIONS

Class Level 2

ANY SPECIES POPULATION

TOTAL POPULATION

ANY SPECIES POPULATION

TOTAL POPULATION

Class Level 3

DIFFERENCES

SIMILARITIES

DIFFERENCES

SIMILARITIES

DIFFERENCES

SIMILARITIES

DIFFERENCES

SIMILARITIES

Class Level 4

Properties of Organisms

Relation to Habitat

KNOWLEDGE SEGREGATED THROUGH CLASSIFICATION

Variation

Patterning over habitat

Class concepts of taxonomy

Floristics and Faunistics

Class concepts of floras, faunas, vegetation and communities

Sequential variation (Evolution)

Continuity of taxonomic classes

Floristic and faunistic history

Continuity of floristics and faunistics

Gene frequency

Ecoclinal unity

Ecotypic unity

Vegetation

Vegetation history

Genetic structure

Community structure

Succession

Fig. 1. Examples of organization of knowledge derived from classification of data from many selective operations. The classes are not intended to be a complete representation of all of those possible, but merely to display the scope of the role of natural selection in biology.

tions, reproductive sequences of populations, communities, vegetation, floristics, and faunistics, it becomes necessary to handle such aggregates of many individuals as classes in our system of knowledge. These classes are established either consciously or intuitively. If a class at a given level rests upon properties of organisms, there is denoted by the class concept thus established a class of organisms possessing these properties. It is assumed that the properties, whether intrinsic or extrinsic, therefore imply the class.

As the empirical data of many selective operations are classified, two major classes develop as viewed in terms of, 1) a set of contemporary organisms (contemporary selections), and 2) a set of organisms in reproductive sequence (sequential selection). Each of these classes of knowledge may be subdivided according to whether it concerns, 1) any given species population, or 2) the total population of diverse kinds of organisms. These two subclasses may each be viewed in terms of differences or similarities observed between members. In some instances further classification may be of value. For example, in the case of contemporary members of a given species population, we might be interested independently in the differences in the properties contingent in the organism and the difference in their habitat relation.

Through classification there is segregated related knowledge about these aggregates or classes or organisms. For example, in the class of contemporary selections of any given species population, there are the facts that permit us to assess differences and similarities of the members. From this observation we may deduce a concept of variation within the species population. By manipulating properties of members of the class, gene frequency may

be measured and the genetic structure of the population determined. The selection of each member by its environment permits us to classify the pertinent facts and relate them to genetic interpretation. However, our case must not be stated in language that appears to raise the selective operation to the abstract class level we have generated and where the results of our comparisons are abstractly unified into concepts. It cannot be over emphasized that it is not the class that was selected, for the class was generated in a classifier's mind. Nor was it the concept that was selected. Only the members of the class could possibly be selected, and these separately and independently. Through them properties are selected.

When the data are considered from the point of view of differences in the relation of members of species populations to environment, we gain a sense of patterning of the population over its habitat mosaic. On the other hand, when the similarities of the members of a species population are considered, the class concepts of the taxonomic class at species or subspecies levels become evident. Considered in terms of like environmental relations, a sense of ecotypic unity of the class may develop.

Also from the point of view of the total unlike population, data may be assessed in terms of differences and similarities of the members. The differences lead to facts of floristics and faunistics, vegetation, and community structure. The similarities provide us with the class concepts of floras, faunas, vegetation, and communities.

It is the sequential classes that lead to the ideas of population continuity and their attendant organism dynamics. From the point of view of any given species population, where we are concerned with differences observed, the facts lead to concepts of evolution and phy-

logenetic change and the role of selection in these changes. Through similarities of constituents such sequences prompt ideas of continuity of taxonomic classes at the species or subspecies level.

These sequences, treated from the point of view of the total population, lead to some of the familiar concepts of ecology. As differences between the members of the sequence are assessed, we are led to ideas of floristic, faunistic, and vegetational change, including succession. On the other hand, as the similarities in the sequence are assessed we gain ideas regarding the continuity of community patterns.

The classes represented in Figure 1 by no means exhaust possible classification of facts derivable from the totality of selections nor are the subjects listed here complete. They are only intended to suggest the kinds of facts available and how they may be isolated and aggregated as objects of inquiry. The main point is that classification is a natural and very important tool of the human mind in organizing data for explanation. Thus the subject matter generally discussed as "natural selection" is here presented in the classes of contemporary and sequential selections as they relate to differences within species populations. Biologists have intuitively and even perhaps unwittingly classified and brought the resulting abstractions to unity. They then have interpreted the classes as though they constituted the empirical data discovered in nature. Following this limited usage there has been a tendency for biologists generally to think of natural selection as a concept more or less restricted to the abstractions of genetics and evolutionary study. It should be apparent to the ecologist, however, that in the various classes segregated are data significant also to his interpretations. In fact, the definition of natural selection as a biological operation permits establishment of the concept as one of the basic propositions for all of biology. Thus perhaps the theory aids as a unifying concept, as well as providing a better perspective for the interrelationships of scientific knowledge with which the biologist works. It is of great importance for the ecologist to integrate properly the role of these organized bodies of knowledge. The interpretation of ecological problems at different levels of abstraction may become clearer if thinking is conditioned by the fact that each and every individual organism is a product of the process of natural selection and *all that it implies*.

Some of the reviewers of our manuscript have suggested that the evolutionist be allowed to retain his usage of the term "natural selection" for selection-like abstractions because he has employed it in this manner for such a long time. To this we object. In his usage "natural selection" is synonymous with evolution and he can only generate a tautology by employing it in the sense of an operation leading to evolution. He says in effect, "Evolution is a product of evolution." The term "natural selection" would be wasted thereby. There is a significant use of the term in precisely the sense that Darwin intended it, and it is this historic use of the term that we advocate.

SUMMARY

Natural selection, being a relation between an organism and its environmental conditions, is an ecological concept. Many ecologists, however, may not have seen the direct role of this concept in their problems because Darwin presented the theory in a context of evolutionary explanation of the origin of species. Subsequent usage has further engulfed the concept with explanations of evolution and cytogenetic operations such that the ecological operations have been obscured. This confusion is primarily a prod-

uct of language and the organization of knowledge. Therefore, language analysis, with its goal of establishing necessary and sufficient truth conditions upon which the concept rests, offers possible clarification of the problem. Semantic analyses of the various conceptions of natural selection display the problems of ambiguities of language. Darwin's conception stemmed from perceptions of different properties and the assessment of their variation and the selective role of the environment in determining which of differing individuals would survive. He abstracted from the natural phenomena only those changed and useful properties which were meaningful to his motive of explaining the origin of species. This led to ambiguity as to whether properties or individuals were being selected and as to the precise locus of the operation. Likewise it resulted in building selection and evolution into a single idea that combined the empirical relations of the individual organism and its environmental conditions with the abstractions of continuity in the variations of successions of organisms.

Subsequent history of the theory has been a continuation and amplification of such ambiguities in language. The population geneticist and evolutionist have added a further level of abstraction by incorporating gene sorting into the concept as an explanation of variations in properties of the language of Darwin. Reproductive continuity is also demanded to insure evolution. Thus, they too have explained evolution rather than described the selective operation at the empirical level.

Semantic analysis establishes the following necessary and sufficient truth conditions for the concept of natural selection:

- 1) It comprises elemental operational (physiological) relations between an individual organism and its environmental conditions such that the organism satisfies all of its physical needs for establishment and survival.
- 2) It endures through the ontogeny of all stages of the life cycle to successor organisms in reproductive sequence, if there are any.

When an understanding is sought for the results of natural selection, as an elemental biological operation, we move from data presented by a single case to that of many like and diverse cases. Our problems shift from perception primarily to classification of conceptual knowledge and the inferences and deductions to be derived therefrom. As the empirical data of many selections are classified, two major classes develop as viewed in terms of a set of contemporary organisms and a set of organisms in reproductive sequence. These classes may be further subdivided in terms of any species population and total population and then by differences and similarities. Thus the data are segregated into classes significant to the role of natural selection in the various disciplines of biology, and thus include the subject matter traditionally discussed as natural selection. Such a conception provides the ecologist with a perspective of the interrelationships of bodies of knowledge which he must synthesize. The interpretation of ecological problems at different levels of abstraction may become clearer if thinking is conditioned by knowledge that each and every individual is a product of natural selection.

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SUMMER PHYTOPLANKTON AT COOS BAY, OREGON

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Few phytoplankton studies have been made of the Pacific Coast of North America (Cupp 1937, 1943); none have been reported for the Oregon coast. This is an investigation of phytoplankton in the Coos Bay, Oregon, region during July and August, 1959. This brief study is intended to serve only as a beginning of phytoplankton analysis in the area. It was made while the author was attending the Oregon Institute of Marine Biology at Charleston with a summer stipend from the National Science Foundation. The author thanks the National Science Foundation, and Dr. Richard Castenholz for his help in diatom determinations and aid in other aspects of the study. Nomenclature follows Cupp (1943).

PROCEDURE, METHODS AND RESULTS

The phytoplankton from 3 stations near the Institute was analyzed once or twice weekly during July and early August, 1959. The first station was in South Slough just south of the Charleston bridge about 0.5 mile from Coos Bay proper in water 3-5 m deep. The second was near the entrance to Coos Bay, northeast of Coos Head in water deep enough for ocean vessels, but protected from heavy wave action. Diurnal tidal movement was very strong at both stations. The third station was in the ocean two miles west of the harbor entrance in water over 30 m deep. Nine samples were taken in the slough, 4 in the bay and 5 in the ocean. The smaller number of bay and ocean samples resulted from poor weather.

Most samples were taken by towing a #20 bolting cloth plankton net for short intervals from a launch, although a few were taken in the slough from a dock which ex-

tended into the main tidal current. Some quantitative samples were taken, but the cells/liter variation was so large that the number proved insufficient for quantitative analysis.

All samples were fixed in 5% formalin and analyzed in the laboratory. At least 140 cells, and usually over 300, were examined from each sample, and the frequencies of all species were determined from this count. In filamentous forms, the individual cells were counted.

Table I summarizes frequency data of the predominant phytoplankton at the 3 stations and Table II compares the average of these figures. All predominant species were diatoms; a single cell of *Ceratium* sp. was the only dinoflagellate observed during the study.

Table I shows that *Coscinodiscus radiatus* and *Chaetoceros decipiens* were the only two species which occurred regularly in ocean samples. The combined frequency percentages of these two individuals varied from 79-99 in all but the August 3 sample. In this sample 3 species, recorded for the first time, predominated. However, the sharp frequency decline at this point of *Coscinodiscus* and *Chaetoceros* is relative, since the number of cells/liter of both individuals was similar to the earlier sample.

At the bay mouth, the predominant diatoms of the ocean station (e.g. *Chaetoceros*, *Coscinodiscus*) and species characteristic of the slough (e.g. *Melosira moniliformis*) were collected regularly.

In the slough, attached diatoms (Laasko 1958) predominated, while the oceanic species were absent or uncommon. The predominant diatom, *Melosira*, was not recorded in ocean samples.

TABLE I. Phytoplankton frequencies from ocean (O), bay (B) and slough (S) samples

Species	DATE AND STATION											
	July 3-9			July 16			July 28-30			Aug. 3		
	O	B	S	O	B	S	O	B	S	O	B	S
<i>Coscinodiscus radiatus</i>	10	11	9	35	62	55	99	—	39	6	47	33
<i>Chaetoceros decipiens</i>	80	70	11	55	24	5	0	—	5	0	0	3
<i>Thalassiosira aestivalis</i>	0	0	0	0	0	0	0	—	0	62	37	0
<i>T. decipiens</i>	0	0	0	0	0	0	0	—	0	18	16	0
<i>Chaetoceros debilis</i>	0	0	0	0	0	0	0	—	0	14	0	0
<i>Melosira moniliformis</i>	0	17	21	0	2	29	0	—	36	0	0	21
<i>Navicula</i> spp.....	0	0	9	0	0	10	0	—	3	0	0	16
<i>Fragilaria striatula</i>	0	0	6	0	0	0	0	—	0	0	0	7
<i>Licmophora abbreviata</i>	0	0	18	0	0	1	0	—	1	0	0	0
<i>Nitzschia paradoxa</i>	0	0	0	0	0	0	0	—	9	0	0	1
<i>Synedra tabulata</i>	0	0	9	0	0	0	0	—	2	0	0	1
Other.....	10	2	17	10	12	0	1	—	5	0	0	18

TABLE II. Phytoplankton frequency and constancy comparisons

Diatom	AVERAGE FREQUENCY			CONSTANCY		
	O	B	S	O	B	S
<i>Coscinodiscus radiatus</i> ...	36.8	45.3	26.4	100	100	100
<i>Chaetoceros decipiens</i>	37.8	29.3	7.1	75	75	100
<i>Melosira moniliformis</i> ...	0.0	5.0	34.7	0	50	100
<i>Thalassiosira aestivalis</i> ...	12.4	9.2	1.2	25	25	17
<i>T. decipiens</i>	3.6	4.0	0.0	25	25	0
<i>Navicula</i> spp.....	0.6	0.3	6.2	50	100	83
<i>Licmophora abbreviata</i> ...	0.0	0.1	4.8	0	50	83
<i>Nitzschia paradoxa</i>	0.0	0.0	5.2	0	0	50
Average No. of species recorded.....	5.4	8.3	9.9			

Table II summarizes these frequencies and lists the constancies from all 3 stations. It can be seen that no abundant species was confined to ocean samples but several were restricted to slough samples. *Chaetoceros decipiens* and *Thalassiosira* spp. were far more predominant at the ocean station, and so are termed oceanic. In contrast, *Melosira moniliformis*, *Navicula* spp., *Licmophora abbreviata* and *Nitzschia paradoxa* were essentially confined to the slough. These littoral species are normally attached to a hard or compact substrate (Laakso 1958). *Coscinodiscus*, on the other hand, the most abundant species, is ubiquitous with respect to these 3 stations.

In 10 samples the number of cells/liter was determined. The values varied from a low of 4 to a high of 337 cells, unusually low figures for oceanic samples (Cupp 1937). No trends were apparent in this sparse and variable data, however.

DISCUSSION

The species composition and frequency figures of the samples examined in this study differ from those taken a

year earlier. Sampling during late July of 1958 showed that the following diatom genera and species were common or abundant at the ocean station: *Asterionella japonica*, *Biddulphia* spp., *Chaetoceros socialis*, *Chaetoceros* spp., *Coscinodiscus* spp., *Coscosira* sp., *Ditylum* sp., *Eucampia* sp., *Rhizolenia* spp., *Skeletonema costatum*, *Stephanopyxis* sp., *Thalassiosira* sp. In addition, the dinoflagellates *Ceratium* sp., *Peridinium* spp., and *Noctiluca* sp. were regular or common.

These differences were possibly accentuated by the different water masses offshore during these two summers. The water mass off the Oregon coast was warmer in 1958 than in 1957. Monthly temperature data of the North Pacific (U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries) indicate that in 1958 the water was approximately 2° F warmer than the 30 yr norm, and that in 1957 it was 2° F colder. Inshore waters, as measured at the Port Orford Fish Dock, Port Orford, Oregon, were about 3.5° C warmer in June, 1958, than in June, 1957.

Inasmuch as phytoplankton communities move with ocean currents, samples from the same station in successive years may represent samples from different communities. Because of this movement, it is impossible to decide whether the successional trend illustrated by the replacement of *Coscinodiscus* and *Chaetoceros* by *Thalassiosira* at the ocean station is actually *in situ* succession or a result of a new water mass bringing in an entirely new community. The sharp changes support the latter hypothesis.

Although most of the diatoms show a preference for either a slough or an oceanic habitat, the bay samples disclose that most frequencies show a continual decline or increase between ocean and slough. Such a change is illustrative of a phytoplankton continuum, well described for terrestrial forest communities by McIntosh (1958). Frequency figures for *Chaetoceros decipiens* and *Thalassiosira aestivalis* illustrate this constant decline from oceanic to slough waters, while the reverse trend is indicated by *Melosira*. Several constancy figures, as well as the average number of species at each habitat emphasize this continuum trend.

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USE IN PLANT ECOLOGY OF CAUSATION, PHYSIOLOGY AND A DEFINITION OF VEGETATION

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Wells (1959) and McMillan (1959a.) have continued a discussion (Major 1958) to which this note adds.

CAUSATION

Wells defends causation as a logical tool. However, causation as "that which occasions or effects a result" (Webster) does not seem applicable by definition to complex systems, such as ecosystems. Something must effect, not affect, a result. If the causation is complex, the "that which" cannot be defined.

Are there really examples of using causation as a logical principle in unraveling ecological relationships which could not more logically be cast into functional form? Causation is not a mathematical concept, and it is only by putting our ecological problems of relationships into mathematical form that we will solve them if we judge by the history of development of other sciences. Admittedly present mathematical formulations of ecology (e.g., Major 1951) are rudimentary. But mathematical notation may be useful in several ways (Lowry 1959). Additionally, mathematically phrased systems suggest some ecological problems that need clarification. An example is the need for definition, both theoretical and empirical, of the flora as an independent factor in an autecological, vegetation, or soil study (Jenny 1958).

Causation demands a sequential ordering of events, and thus makes seemingly illogical our untangling a logical knot by reversing a supposed chain of causation. Such reversals have been very effective in ecology. For example: 1) Speciation is supposed to result in genetic isolation of taxa. While this is a productive idea for abrupt speciation, the reverse is more productive for gradual speciation.

2) Genetically controlled ecotypic variation influences ecological behavior of taxa, as Kruckeberg (1959) emphasizes. If the ecological behavior be used as a measure of habitat, then the reverse of Kruckeberg's statement is a good paraphrase of Turesson's (1922:112) original definition of the ecotype as "the genotypical response of an ecospecies to a particular habitat."

3) Vegetation forms soil. Vegetation does contribute organic matter to weathering rock and thereby forms soil, but the soil also nourishes vegetation. The Great Soil Groups are not at all correlated with vegetation formations. Podzols are found under grassland, heath, brush, broad-leaved, and coniferous trees; prairie soils under grassland and brush, etc. It seems more logical to consider both vegetation and soil as parametric functions of the independent factors determining the entire ecosystem (Jenny 1941, Major 1951). Very many cases are known where a soil difference correlates with a vegetation difference. This is not very helpful in explaining either. However, both differences can be correlated with an ecosystem variable defined to be independent such as soil parent material, regional climate, slope exposure, snow accumulation, etc.

4) Microclimates determine vegetation differences. Plants of small stature do respond to the changes in regional or local climates produced by larger plants, such as a forest canopy, but it is these larger plants which modify the atmospheric conditions.

5) Topography determines vegetation. Vegetation on north and south slopes is usually different, but sand dunes

and loess both seem to be collected by vegetation to yield distinctive topographic forms.

6) Abundant soil organic matter produces an extensive root system. Agricultural crops do produce better root systems in more fertile soils, but the high organic matter content of chernozems is probably a function of extensive grass root systems.

7) High soil nitrogen produces large plant yields. This is an agronomic axiom, but some peaty soils contain great quantities of total N on a volumetric basis and produce very little plant growth. Their high N content is a function of slow rate of decay of the organic matter added to the ecosystem by the bog vegetation.

8) A given soil pH is causally related to the occurrence of a particular plant species. Plants do show pH optima, especially under interspecific competition, but the addition of H⁺ ions and withdrawal of metallic cations by plants changes substrate reaction.

9) Forest fires produce a human population without opportunities for expression, poverty in a word. True, but the reverse is also true.

10) Ditto for soil erosion.

11) Snow accumulation determines vegetation differences. This is a first principle of arctic and high mountain ecology, but on the Wasatch Plateau of Utah and in similar subalpine areas islands of conifers form snowdrifts. The vegetation of snow accumulation areas on the Wasatch Plateau is not trees but a tall herb community.

12) Saline soils select out halophytic plants from the regional flora, but some halophytes actively salinize the soils in which they grow by accumulating salts in their deciduous leaves.

13) High concentrations of gophers, rabbits, ground squirrels, etc. bring about poor range condition. Rodent concentrations and poor range conditions are often correlated, but the reverse chain of argument is more useful as a range management concept.

Other examples could be given.

We would simply not need to make these mental reversals if the ecological relationships were thrown into functional form. Once the relationship is established, study of mechanisms can follow without the infinite regress which causal chains of argument involve.

Causation is evidently analogous to teleology as an explanation of ecological events. Both attempt to describe a mechanism, process, or reason for reaching a known state of affairs—but the process is really unknown. Thus, organisms' evolution toward fitness to their environment is an established fact, but the processes leading to such fitness were hardly more cleared up by Darwin's causal hypothesis than by teleological explanations. Darwin's really wonderful contribution was a generalization of described facts, not a causal explanation. It seems that "directing forces" in nature turn out on analysis to be simply descriptions of things as they are.

It must be admitted that by closer definition of the terms in the above examples, the reversals suggested could be seen to involve quite different events and processes. Nevertheless, speciation is as broadly defined as suggested in 1); soil and vegetation have had both morphological and chemical definitions as in 3); in 8) and 9) poverty can be intellectual and material; snow accumulation as in 11) by an obstacle to the saltating

and air borne movement of wind-carried snow is really quite different from the accumulation of snow by general stiling of a current of snowbearing air by major topographic features, and the difference is shown by original grain sizes, firnification rates, settling, formation of scoured depressions, etc., but still an ordinary snow survey would simply show more water equivalent than normal in both areas; etc.

Again, to set up some factors as independent and others as dependent is almost to imply causation of the latter by the former. There is this important difference however. The yield of vegetation, for example, as a dependent factor is dependent not only on, say, variations in an independently varying climatic factor but also on the actual states of all those other factors defining the ecosystem which are of necessity being held invariant, at some particular level, while the given climatic factor is allowed to vary. A functional scheme makes such situations clear, and a causal scheme does not.

This is not a semantic discussion. A consequence of use of functional arguments is acquaintance of ecologists with mathematics.

PHYSIOLOGICAL ECOLOGY

Wells (1959) accords a basic position to plant physiology, even in ecological study. In their training as botanists ecologists acquire some basic physiological knowledge of plant functions, but the hope expressed in the title to Schimper's classic *Plant geography upon a physiological basis* has not been fulfilled (Tansley 1939: 527, 1920:128).

As a matter of fact, Raup (1942:330) believed the assumption of causal physiological relationships between plants and their environments was a basic mistake in the development of plant ecology and still vitiates it (pp. 338-9, 348, 350). This assumption is not a necessary one. The one assumption necessary to ecology is that plants are related to environments, and the one assumption necessary to plant sociology is that similar associations of plants occur repeatedly. No causation is involved in these basic assumptions and no physiology. Both assumptions seem to be facts to most field botanists. Both studies can rely exclusively on field observations for data. They can dispense with theoretical constructions.

Explanations of the relationships found—of plants to environment and of plants to one another—will come from morphological, physiological, historical, genetic, and chorologic studies. Explanations are of course impossible without theory.

Plant physiology has some real deficiencies from the viewpoint of the ecologist and plant sociologist. The variety of plants exploited is pitifully small. It does not include the plants of most phytogeographical interest (Lavrenko 1947:11). Plant physiologists do not define ecosystems. We now know that plants grow where they do not only because these ecosystems fit within their physiological spans of tolerance, but also because other plants do not crowd them out there. Until physiology presents data on plants competing with each other in defined ecosystems, physiological data will continue to be necessary but quite insufficient to solve autecological problems. And little more progress has been made in study of the physiology of vegetation in the two decades since Tansley (1939) complained of this neglect.

In considering the role of plant physiological data in elucidating forest successions, Decker (1959), as a physiologist presumably, concludes that more autecological studies are necessary to give the framework within which physiological data can find use.

If the above arguments are accepted, we must conclude that definition of vegetation is of importance to plant ecologists, including those primarily interested in plant physiology. Vegetation, after all, is the habitat within which plants live. When the ecologist defines habitats, he must define vegetation.

VEGETATION

Ehrendorfer (1954:152) defines a biocoenose as a "concrete, spatially limited community of various organisms which are more or less strongly bound together mutually and with their environment through eco-physiological ties and relationships." He compares this concrete object of study with the object of taxonomic study, defining species as sexually reproducing and separated by sterility barriers. Then Ehrendorfer is able to show with impeccable logic that species do not form a continuum and therefore may be considered concrete, absolutely separated units. They could be arranged in a phylogenetic hierarchy if only we had more knowledge of phylogeny, there were a more perfect correlation between relationship and similarity, and definition of the abstract systematic categories were not necessarily more or less rigid. On the other hand, biocoenoses do form a continuum composed of one to several kinds of organisms and numbers of individuals and with a continuum of biotic and/or physical factor relationships to environments. Therefore biocoenoses are not stable in space or time, are not closed. Their relationships are multidimensional in terms of environmental factors (Major 1951). Their members have very unequal community-determining values (determinants of Sukachev 1929:303 *et seq.*, edificators² of Lavrenko 1947), constructiveness (Braun-Blanquet 1951:451 following Pavillard), indicator value, constancy, and fidelity. Thus no hierarchical classification of biocoenoses is deemed possible.

Ehrendorfer's conclusion and his contrast between biocoenose and species follows from his definitions. These are disparate. His definition of a species is an ideal, theoretical one which cannot be applied to most species in our floras given present knowledge; his definition of a biocoenosis is a generalized, empirical one which ignores theory derived from field experience. Thus, we know of many sterility barriers within what we now call species; we know of many fertile hybrids between "species"; and between the individuals of many "species" there can be no sexual relationships at all. There are all grades of relationship from reticulate to complete isolation both within and between what we now say are species. As to biocoenoses, if the reality of reactions between members of the community and between them and their environment be added to Ehrendorfer's definition, then we have a theoretical reason for the observed discontinuities between communities in nature and the observed marked stability both in space and time of associations of plants and animals. In other words, under Ehrendorfer's original definition the biocoenosis is not more than the sum of its parts, can be subdivided indefinitely without losing its characteristics, and its parts have no specific mutual relationships—they do not mutually direct or control each other and lose their character when separated from the whole (Niggli 1949:42). All the above 3 points are denied by field experience, but if a biocoenosis is defined so its organic members mutually react, the definition will fit field experience. See Tuxen (1957) and Sukachev (1950:456) for such definitions based on just such experience.

It appears to the writer that McMillan's definition of vegetation (1959a), considered here as the expression of the plant communities of an area, is as loose as Ehren-

² In the archaic sense of the English word.

dorfer's. For example, to consider one plant growing alone is quite unnatural. It is a very special case. Most plants actually grow with other plants in a habitat whose operational properties (Mason and Langenheim 1957: 331) are at least partially a function of the associated plants. Almost universally, e.g., a local climate is modified as to precipitation, interception, radiation to and from the ground surface, and temperature gradients by associated plants to produce a microclimate in which the individual plant lives. We can only with difficulty measure such microclimates, much less reproduce them for experimental work with plants. Kittredge (1948) and Geiger (1950) have written books on this subject of forest influences, and many are adding to its facts and interpretations. Such influences of plants on their habitats are not limited to forests. They are of general occurrence, and on their recognition Sukachev (1929) based his classification of site factors into exogenous and endogenous, independent properties of the environment and dependent properties of the community in other words (Major 1951: 395). Tansley's (1954:157) allogenic and autogenic factors and Fries' (1925) primary and secondary express the same idea.

Just as with species, there is excellent reason for using the tightest definition possible of a biocoenose—with special cases considered as such. Single plants, artificial aggregations not found in nature, garden cultures are phytosociologically such cases. They may very well, of course, give valuable phytosociological and ecological data not obtainable at all from natural plant communities (Tüxen 1955, McMillan 1959b).

However, it is very difficult to transfer data obtained in artificial ecosystems to the ecology of natural ecosystems. One reason is our current lack of descriptive data on natural ecosystems. A distinguishing feature of most English and American ecological work is its lack of community description in the form of stand survey tables. These stand survey records can be arranged in associations, formations, continua, gradients, landscapes, sequences, or functions. They may be used to demonstrate various ecological series, chorological spectra, successional relationships, community structure, composition, history of the addition of various floristic elements to the local flora, vegetation classification, and even comparative physiology.

The above relationships and points of view have been developed using all the crudities of present knowledge of species. If we attain, as McMillan suggests (1959c: 521), the use of infraspecific variations in ecology by developing, among other things, an adequate system of recognition, classification, and nomenclature for them, understanding of vegetation will be immeasurably refined.

McMillan (1959a) appeals to the free choice of a system under which to work which is open to ecologists. The choice is not absolutely free. The system must fit current scientific theory and agree with both observation and experiment. It should be aimed to at least potential completeness. These are important limitations to the ecologist's comfort. Disregarding vegetation should make all botanists, but especially plant ecologists, uncomfortable.

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LIVING STUMPS IN THE SIERRA NEVADA

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INTRODUCTION

In a dense forest that has been thinned recently there are often some tree stumps that are still alive and growing despite the loss of their green tops. Such stumps have been noted for many years and are known to be products of root-grafting between trees (Bormann and Graham 1957).

If light cutting or windfall occurs in a dense stand where root-grafting is common, food materials in the standing members of a grafted clump will move through root-grafts into the fresh stumps. Thus the cambium of a stump can continue to add increments of wood and bark.

This paper reports on studies of the properties of living stumps, their longevity, and their growth. Data are based on above-ground examinations of 25 living stumps of 6 species of Sierra Nevada conifers, and cursory observations of several dozen others. The stumps are on the La Porte Ranger District of the Plumas National Forest in California. Several are within the Challenge Experimental Forest which is operated by the Pacific Southwest Forest and Range Experiment Station.

GENERAL CHARACTERISTICS OF LIVING STUMPS

As a stump grows, a ring of callus tissue usually forms around its top. This callus sometimes grows across the entire cut surface, thus sealing and protecting it. Such

capped stumps become impervious to fungus and termite attack and may exhibit remarkable longevity (Fig. 1). Sugar pine stump No. 1 and red fir No. 9 (Table I) were completely capped.



FIG. 1. Douglas-fir living stump almost completely callused over. The tree was felled 17 years ago. Host tree is in left background.

TABLE I. Detailed measurements of living stumps

Species	STUMP			Tree age	Stump age	Tree rings per inch	Stump rings per inch	Width of new growth	Host distance	Probable crown class
	No.	Height	Dia.							
Sugar pine (<i>Pinus lambertiana</i> Dougl.)	1	<i>Ft.</i> 2.5	<i>In.</i> 28	<i>Yrs.</i> 75	<i>Yrs.</i> 17	<i>No.</i> 7	<i>No.</i> 19	<i>In.</i> 0.89	<i>Ft.</i> 3	Int.
	26	0.5	10	65	18	22	45	0.40	6	Sup.
Ponderosa pine (<i>Pinus ponderosa</i> Laws.)	2	2.0	28	50	23	4	64	0.36	3	Dom.
	3	3.0	21	75	17	4	113	0.15	4	Int.
	20	3.5	16	55	30	9	50	0.60	4	Sup.
	21	3.5	20	70	12	14	171	0.07	7	Int.
	22	3.0	20	70	15	7	100	0.15	6	Int.
California red fir (<i>Abies magnifica</i> A. Murr.)	5	1.5	13	70	20	14	34	0.59	2	Sup.
	6	1.0	8	70	22	25	28	0.78	3	Sup.
	7	2.5	15	60	22	12	51	0.43	1	Sup.
	8	4.5	16	70	10	11	50	0.20	3	Int.
	9	2.5	21	40	61	5	36	1.70	5	Int.
White fir (<i>Abies concolor</i> (Gord. & Glend.) Lindl.)	19	2.0	13	35	45	16	64	0.70	1	Sup.
	25	3.5	20	200	13	44	17	0.75	4	Sup.
Douglas-fir (<i>Pseudotsuga menziesii</i> (Mirb.) Franco)	10	9.0	36	70	22	—	33	0.66	1	Dom.
	16	3.5	26	—	53	—	28	1.90	4	Codom.
	17	2.5	18	60	17	13	24	0.70	3	Int.
	18	3.0	33	120	87	—	38	2.30	1	—
	23	7.0	34	60	30	10	30	1.00	2	Codom.
	24	3.0	19	50	15	10	23	0.65	23	Dom.
Incense-cedar (<i>Libocedrus decurrens</i> Torr.)	11	2.5	19	50	20	7	24	0.85	11	Int.
	12	1.5	20	50	21	7	24	0.88	7	Int.
	13	1.5	20	50	22	13	18	1.20	6	Int.
	14	0.5	10	45	27	19	59	0.46	7	Sup.
	15	3.0	18	50	22	22	22	1.00	12	Dom.

On some stumps only one major root is translocating food from one or more host trees. In this case only that sector of the stump directly above the root remains alive (Fig. 2).



Fig. 2. Douglas-fir living stump grafted on only one side. The host tree shown in background is 10 ft distant.

The bark of a living stump is distinctive for its "normal" or "live" appearance which contrasts strongly with the lackluster look of typical dead bark. Occasionally a heavy flow of pitch may issue from cracks in the bark or callus.

Because it is encased in new wood and bark, the old wood in living stumps is often well preserved (Fig. 3). The cutting that produced the stumps shown in Figures 1-3 also left many "dead" stumps. After 17 years the standing dead ones could be torn apart easily while the living ones would still resist axe blows on the old exposed surfaces.

The wood of the living shell gradually differentiates into heartwood and sapwood. Thus a radial section from the pith outward discloses original heartwood, original sapwood, new heartwood, and new sapwood. This pattern is especially marked in Douglas-fir (*Pseudotsuga menziesii*) and the true firs (*Abies* sp.).

DETAILED STUMP MEASUREMENTS

In assembling the data presented in Table I measurements and estimates were made according to the following criteria:

Height—From highest point of living tissue to the ground, to nearest $\frac{1}{2}$ ft.

Diameter—Taken below undercut on cut stumps, at



Fig. 3. Radial section through Douglas-fir living stump showing condition of wood and change in growth rate since tree was felled. Note differentiation of new wood into heartwood and sapwood. This is stump No. 17 in Table I.

breast height on taller natural stumps. Given to nearest inch.

Tree age—Estimated age of tree at time of felling, from ring counts.

Stump age—Number of annual rings counted in living shell.

Tree rings per inch—Number of rings in last radial inch of tree prior to felling.

Stump rings per inch—Average number of rings per inch of new growth.

Width of new growth—Thickness of new growth (new xylem), to nearest 0.01 inch.

Host distance—Distance to nearest tree of same species, exclusive of seedlings and saplings, to nearest foot.

Probable crown class—An estimate of former crown position made by observing stump size and original growth rate compared to those of likely hosts, and observations of the crowns of neighboring trees still standing.

DISCUSSION AND CONCLUSIONS

The data in Table I indicate that even within a species, living stumps are highly variable. They can be initiated in trees as young as 35 years (white fir No. 19) or as old as 200 (white fir No. 25). One stump has persisted for almost a century (Douglas-fir No. 18), and a record exists of a Douglas-fir living stump persisting more than 200 years (Newins 1916).

Although living stumps have no green tops, water and food materials can be transported to heights of at least 9 ft (Douglas-fir No. 10).

Growth in the new tissue is usually, but not always, slower than in the tree before felling. In incense-cedar No. 15 the growth rate stayed about the same; in white fir No. 25 it almost tripled. Incense-cedar and Douglas-fir show the least change in growth rate, and ponderosa pine the greatest. The growth rate may be influenced by the size and number of sustaining root-grafts, or the number and vigor of the host trees. Former crown class may also be involved though these data are inconclusive.

The age of new growth may be determined by examining an increment core under low magnification. Ring spacing normally shows an abrupt change, marking the time of felling, and the old wood is either rotten, or in the pines, blue-stained or impregnated with pitch. How-

ever, even under magnification the age of some cores is difficult to establish because of the lack of contrast between springwood and summerwood. This is especially true in incense-cedar.

Most of the living stumps examined were within 6 ft of the nearest likely host, but two were more than 10 ft distant and one was 23 ft away. These are minimal distances; the stumps may have been root-grafted to trees further away than those judged the likely hosts. Indeed, there is a Douglas-fir living stump shown by root excavation to be grafted to a tree 50 ft away (Pemberton 1920). All 6 species mentioned in this report are probably capable of forming root fusions at the spacings commonly used in plantations.

Crown position is apparently not a factor in determining whether a cut tree can give rise to a living stump. This suggests it is not necessarily true that within a grafted cluster dominant trees pass on materials to suppressed trees, or vice versa, as has been suggested (Bormann and Graham 1959 Kuntz and Riker 1956). A considerable proportion of the stumps were from trees that were co-dominant or dominant before they were felled. Several of the stumps listed in Table I were created by a pole and piling harvest which tends to select smaller trees with little taper (inferior crown classes). Hence the trees in Table I may not be representative of all crown classes, yet despite this, dominants and codominants are well represented too.

Felling method is not a factor in the possibility of a living stump being produced. A saw-cut is probably most likely to heal over because it seldom disturbs the

cambium below the cut surface, but even ragged axe-cut stumps can stay alive (stumps Nos. 25 and 26). The splintered stubs of wind-felled trees are least likely to live but even they are represented by stumps Nos. 10 and 24 (Fig. 4).

To cover a stump the callus tissue must grow along a solid surface that can support it. If the center of the stump rots out before the callus reaches that area, horizontal growth is then replaced by growth downward into the hollow. In extreme cases where rot outpaces new growth considerably, the callus may grow down into the hollow along the inner wall of the living shell. In Douglas-fir No. 16 this occurred, and the stump is a hollow shell, lined with bark inside and out. Stumps like this frequently accumulate litter in their hollow centers, and so provide a seedbed for tree or shrub seedlings.

A root-grafted tree, when cut, does not always give rise to a living stump. During logging operations many stumps are stripped of their bark or splintered and mashed by moving logs and equipment. Their cambium is exposed to the air, and the cambial cells dehydrate. In the Sierra Nevada, fresh pine stumps are commonly attacked by the red turpentine beetle (*Dendroctonus valens* Lec.), whose larvae kill the cambium by girdling. This may be the cause of wholly dead trees and stumps whose grafted roots still live, a phenomenon reported by Bormann and Graham (1959).

In an old stand if the last surviving member of a root-grafted cluster is cut, its stump cannot continue to live though in the past it may have been joined to several other trees. Nor can any stand produce living stumps if it is cut too heavily. For these reasons the frequency of living stumps can be used as an index to the frequency of root-grafting only in lightly cut stands. There will always be more root-grafting in a stand than the numbers of living stumps indicate.

One interesting problem concerning living stumps is the means by which solutes are available to them. Because there is no green top, all manufactured foods must come through root-grafts from hosts. The lack of a top also excludes the possibility that solute movement is effected by transpiration pull or sap cohesion. The manner by which solutes move in trees is controversial. Living stumps may be valuable aids in the study of various theories which have been suggested for this phenomenon.

When a thinning is made, it is possible that the residual stand benefits from the formation of living stumps. To the forester concerned with timber culture, two possible effects seem preeminent and need further study: the effect on the host tree's growth rate, and the role of living stumps in restraining rot.

Because the living stump is maintained by nearby standing trees, it would be expected to exert a measurable influence on the growth of those trees. Terming these trees "hosts" does not infer that the living stump is a parasite on its neighbors, draining them of some of their vigor. There is no evidence that such a simple relationship exists; in fact, exactly the opposite may be true. For example, the root system of the living stump may contribute greatly to the absorptive capacity of the hosts. This may outweigh the parasitic effect, which is normally adequate for only token growth (Table I).

The implications of this possibility enter any situation where there is root-grafting. The use by a standing tree of the root system of a cut tree could help to explain why "thinning from below" (e.g. removal of trees of inferior crown classes) sometimes results in increased growth of the residuals. It may also explain the remarkable growth, after removal of dominants, in trees known to have been suppressed for many years.



FIG. 4. Naturally formed living stump of Douglas-fir. The tree was felled by wind. This is tree No. 10 described in Table I.

The role of living stumps in restraining the spread of rots is speculative. However, the "pipeline" function of root-grafts in spreading diseases from one tree to another has been reported in oak wilt where the movement of spores takes place through grafts (Kuntz and Riker 1956); and even fungal hyphae can spread through grafts by breaking down the cell walls of uninfected joined trees (Hafiz Khan 1910). Also living stumps are usually more resistant to rots than their dead contemporaries. Some are probably completely impermeable by virtue of a perfect callus cover. If such stumps had not lived, would the rot in their progressively deteriorating roots have spread to those of the host? Can the incidence of root rots in grafted stands be retarded by encouraging the formation of living stumps after thinning?

These questions can be answered only by further investigation.

SUMMARY

1. Twenty-five living stumps of ponderosa pine, sugar pine, Douglas-fir, incense-cedar, white fir, and red fir were examined on the westside Sierra Nevada.

2. Most of the living stumps followed logging but two occurred where the original tree was wind-felled.

3. Wood laid on after felling differentiates into heartwood and sapwood.

4. The oldest stump observed had persisted for 87 years; the tallest was 9 feet.

5. Original crown class does not govern the possibility of a root-grafted stump remaining alive.

6. Living stumps may serve a useful function in providing extensive root systems to residual members of the grafted cluster and in slowing the tree-to-tree spread of root rots.

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GROWTH FORM OF CRESTED WHEATGRASS AS AFFECTED BY SITE AND GRAZING¹

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INTRODUCTION

Growth characteristics within a species vary widely in response to variations in environment. Not only does the plant environment in a mountainous country change abruptly with elevation, but it also varies locally from site to site, depending primarily upon microrelief, slope and exposure, nature and depth of soil, and particularly on the supply of moisture. Clark (1945) concluded that a marked variability in the growth characteristics of range grasses was the rule rather than the exception.

Many investigators have studied height-weight or height-volume relationships of grasses as a basis for determining production or utilization (Campbell and Crafts 1938, Collins and Hurtt 1943, Crafts 1938, Lommason and Jensen 1938, Lommason 1943, Reid and Pickford 1941, and Valentine 1946). Various graphs,

conversion tables, and slide rules were developed from these relationships as aids in converting stubble height directly to utilization percentages. At first, the method met with notable success because of its simplicity and relative speed. But later on, several investigators pointed out a principal weakness in the method, mainly that variation in the growth characteristics of a species make data collected in one area useless in another (Clark 1945, Heady 1950, McArthur 1951, and Heady 1957).

The term "growth form" in this paper refers not to a height-weight relationship alone—as the word has been used in the work with forage production and utilization—but to the actual shape of the aerial or above-ground part of the grass plant in the field. Thus, the growth form of a crested wheatgrass³ plant describes the divergence from the perpendicular of the aerial canopy and may be defined as being erect, semispreading, spreading or prostrate. Variations are readily observed and appear to be influenced by past intensity of grazing and by differences in environment. This complicates the task of developing methods for estimating weight of herbage produced and degree of utilization based on individual plant measurements.

³ Crested wheatgrass refers to *Agropyron desertorum* (Fisch.) Schult. The U. S. Department of Agriculture's Committee on Plant Nomenclature recommended on March 27, 1956, that *A. desertorum* be designated as crested wheatgrass and *A. cristatum* (L.) Gaertn. as fairway wheatgrass.

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² Central headquarters maintained in cooperation with Colorado State University. Research reported here was conducted at the field research center located at Albuquerque, New Mexico in cooperation with the University of New Mexico.

Consequently, the objectives of this study were to evaluate the causes for these variations in growth form; that is, the effect of different sites and different intensities of past use, and to find a means of accounting for these variations so that plant measurements taken from different areas could be compared.

LOCATION AND DESCRIPTION OF EXPERIMENTAL SITES

Data were collected in experimental pastures on seeded ranges at Cebolla Mesa, No Agua, and Laguna Seca in north-central New Mexico.

Cebolla Mesa

Cebolla Mesa, 20 miles north of Taos, New Mexico, at an elevation of 7,450 ft, has an average annual precipitation of 12.5 in. In 1956, annual precipitation was only 7.3 in., and in 1957, the year of this study, it was 18.3 in. One-third of the annual precipitation is received during the 6 months over-winter period, October through March. The area supported big sagebrush (*Artemisia tridentata* Nutt.), pinyon pine (*Pinus edulis* Engelm.), Utah juniper (*Juniperus osteosperma* (Torr.) Little), and one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg. before the openings were plowed and seeded to crested wheatgrass in 1947. Grazing by cattle was started in the spring of 1949. Beginning in the spring of 1952, three 40- to 50-acre experimental pastures were fenced and grazed at different rates. Utilization of crested wheatgrass through 1957 for the three pastures averaged 40, 54, and 70%. Cattle-proof enclosures one acre in size were installed in 1953 within each pasture.

No Agua

The No Agua site is in the lower fringe of the ponderosa pine zone. It was plowed and planted to crested wheatgrass in 1949; previously it had supported various rabbit brush (*Chrysothamnus* spp.), broom snakeweed (*Gutierrezia sarothrae* (Pursh.) Britt. and Rusby), pingue (*Hymenoxys richardsonii* (Hook.) Cockerell), and an unthrifty stand of blue grama (*Bouteloua gracilis* (H.B.K.) Lag.). The area is 5 miles north of Tres Piedras at an elevation of about 8,300 ft. Average annual precipitation is 13.3 in.; in 1956 it was 6.1, and in 1957, 18.7 in. Long-term U. S. Weather Bureau records show that over-winter precipitation, October 1 to April 1, averages 37% of the annual total. Three experimental pastures, each 12 acres in size and containing 1 acre enclosures were fenced in the spring of 1955. Average utilization by cattle for the 3 years, 1955 through 1957, was 36, 62, and 77% by weight of the total herbage produced by the plants.

Laguna Seca

Laguna Seca at 7,400 ft elevation is in the transition between the ponderosa pine and pinyon-juniper zones. It has a long-time average precipitation of 16.5 in., of which 42% falls between October 1 and April 1. The total annual precipitation was 8.0 in. in 1956 and 22.7 in. in 1957. This area, about 40 miles north of Cuba, was plowed and planted to crested wheatgrass in 1950. Before it was seeded, the study site supported mainly sagebrush and rabbitbrushes and a sparse understory of grasses, such as blue grama, western wheatgrass (*Agropyron smithii* Rydb.) and bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J. G. Smith). The experimental site had been grazed by cattle at an average of 20% utilization since 1952.

METHODS OF STUDY

Individual plants of crested wheatgrass were measured in 1957 at all three study areas. Plants measured were

growing within randomly selected sample plots in different pastures and enclosures of each study area to represent differences in past grazing treatment. As a result, plant measurements reflect not only differences in climatic, soil and other environmental factors among the three sites, but differences in past grazing as well. At the beginning of the growing season, wire cages were placed over the sample plots to protect them from grazing. It was found, with the exception of young seedlings, that field measurement could not be taken consistently closer than the nearest 0.2 in.

Seven measurements of each plant were made. Four of these measurements were on undisturbed plants in their natural field position:

1. Basal Diameter: Diameter of the base of the plant was taken at ground level. If the base were circular, one measurement was taken, but if it were oblong or rectangular several measurements were averaged.

2. Crown Diameter: Diameter of the canopy or aerial spread was measured. For circular crowns, one measurement sufficed, but for other shapes averages of two measurements were used.

3. Leaf Height: According to a definition by Heady (1957), "height is defined as the perpendicular distance from the soil at the base of the plant to the tallest aerial part of the plant in its natural position. The method of measuring height is to place a ruler alongside the plant to be measured and to read the height in its natural position." This measurement represents the height of the tallest leaf collar above the ground. The heights of leaf tips were not measured because their position varied with the time of day, moisture conditions, wind, and other factors. Collar height appeared to be least influenced by these agents.

4. Culm Height: This measurement was made from the soil to the tip of the tallest culm. No discernible variation due to time of day or moisture conditions was observed in culm position.

Three measurements were taken after foliage and culms were raised to the maximum vertical position and grasped together by hand at average leaf height. These are called compressed measurements:

1. Compressed Crown Diameter: Diameter of the compressed aerial part of the plant was measured at the average height of the leaf collars.

2. Compressed Leaf Length: Length to the tallest leaf collar in the compressed position was measured. "Length of leaves as distinguished from height is obtained by straightening the plant to its fullest length and measuring that length with a ruler placed alongside the plant. This measurement eliminates the concept of natural position and should be described as length even though it may be height in some cases" (Heady 1957).

3. Compressed Culm Length: This was the length to the tip of the tallest culm with the plant in the compressed position.

These seven measurements were selected because they are relatively free of personal judgment and easy to take. Similar measurements can be obtained by future workers. The only measurement that might be considered arbitrary and therefore subject to bias and error is compressed crown diameter at "average" height of the leaf collars. Since the range in height of leaf collars is usually no more than 1 or 2 in., the position of this measurement offers no serious problem.

The seven measurements were made on two different groups of plants collected one month apart in each of the three areas. The first group consisting of 9,603 plants

was measured in June. The second consisting of 823 plants was measured in August.

Analyses of variance of culm length, leaf length, and the differences between compressed and uncompressed measurements were computed. Differences between all pastures in each area were tested by "Student's" *t* test. Limits of 99 to 1 were used to test significance.

RESULTS

Crested wheatgrass had an entirely different growth form on each of the three sites studied. Under the more moist conditions at Laguna Seca, the plants grew perpendicular to the ground, with little aerial spread so that no significant change in form was caused by compression. At the drier No Agua site, the plants diverged from the perpendicular, had a large aerial spread, and showed a significant change in growth form when compressed. At Cebolla Mesa, the driest site, the plants had a distinct spreading form, a large aerial spread, and an even greater change in form under compression. The percentages of plants having increased or decreased height measurements when compressed also indicated that growth form becomes progressively more spreading in the drier areas. When various ratios of crown diameter, basal diameter, and leaf length measurements are compared, the effects of site differences on growth form are apparent (Table I). Variations in growth form between sites may be defined as erect, semispreading, and spreading (Fig. 1).

TABLE I. Average ratios between crown diameter, basal diameter, and leaf height of crested wheatgrass at three sites in northern New Mexico

Ratio	Cebolla Mesa	No Agua	Laguna Seca
Crown diameter Basal diameter	4.196	2.822	2.546
Crown diameter Leaf height	.702	.556	.555
Basal diameter Leaf height	.167	.197	.218

Growth form at any one site varied with the degree of past utilization by cattle. Differences due to intensity of grazing were greater than differences due to site. Plants heavily grazed in the spring, from which 70% of the herbage was removed, diverge from the erect position enough to be called prostrate. No plants on ungrazed sites had a growth form this extreme. Heavily grazed crested wheatgrass plants regardless of area, more closely resemble those in the drier sites in growth form; those grazed less heavily had a more erect, less spreading form that closely resembled plants in the more moist area. Several years of heavy use (removing 70% or more of the herbage yearly) resulted in plants with a prostrate form in all specimens studied or observed.

A distinct difference in culm lengths was found between the 3 sites, but no difference was found between the different intensities of grazing within any one site (Table II). Therefore, culm lengths could be used as an indicator of moisture conditions between sites but would be a poor indicator of past grazing treatment. This might possibly be due to a tendency for the less vigorous plants to progressively expend their last stored energy in sending up seed heads.

There was a distinct difference in leaf length both between sites and between pastures within a site. There-



FIG. 1. Growth forms of crested wheatgrass: A, Erect, B, spreading.

fore, leaf length is an indicator of site differences as well as an indicator of differences due to past grazing treatment.

TABLE II. Average basal diameters and leaf and culm lengths of crested wheatgrass grazed at different intensities at three locations in northern New Mexico

Location	Mean utilization	Plants	Basal diameter	Leaf length	Culm length
	Percent	No.	Inches	Inches	Inches
Cebolla Mesa.....	0	523	2.16	8.72	11.20
	40	1,051	2.01	7.96	10.16
	54	1,373	1.35	7.92	10.46
	70	1,045	.86	7.33	9.97
No Agua.....	0	530	2.17	10.54	13.62
	36	560	1.69	9.26	13.64
	62	619	1.32	8.20	11.91
	77	544	1.32	9.00	11.95
Laguna Seca.....	20	3,358	3.36	13.82	20.18

Compression was found to be a good means of minimizing differences in growth form of crested wheatgrass when making plant measurements. Compression of a plant having a perpendicular or erect growth form and a small basal diameter resulted in no change in leaf length, while compression of a perpendicular plant having a large basal diameter resulted in a loss of leaf length. Compression of a plant having a spreading form always resulted in a gain in leaf length regardless of the size of the basal diameter. This gain increased proportionately as the plant became more spreading. In future attempts to express height-weight or height-volume relationships, differences in growth forms should be recognized as important. This study indicates that compression is an effective means of eliminating these measurement differences.

SUMMARY AND CONCLUSIONS

Seven measurements were taken of 10,426 individual crested wheatgrass plants growing at 3 sites in north-central New Mexico. The main objective of this study was to determine the effect of sites with different precipitation and different intensities of past grazing by cattle on growth form. Conclusions drawn from the study were as follows:

1. Crested wheatgrass has a more or less perpendicular growth form when not grazed. On dry sites, crested wheatgrass is more spreading than on moist areas grazed at similar intensities.

2. Growth form, which tends to be more perpendicular with increased moisture, becomes progressively more spreading with increased intensities of cattle grazing until a prostrate form may result under grazing where 70% or more of the herbage is removed yearly.

3. Past intensity of cattle grazing has a greater effect upon the growth form than does site.

4. For measurement purposes, differences in growth form may be minimized by compressing the aerial parts of crested wheatgrass. Foliage and culms are raised to the maximum vertical position and grasped together at average leaf height. Compression, therefore, facilitates the comparison of plant measurements of height and width taken on plants undergoing different intensities of grazing or growing under different precipitation conditions.

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ESTIMATION OF NET PRIMARY PRODUCTION OF FOREST AND SHRUB COMMUNITIES¹

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Despite the current interest in productivity, one major group of natural communities—those dominated by woody plants—has largely resisted effective productivity measurement. Complexity of structure and size of plants in forests render such research difficult, though not impossible as indicated by work of Burger (1953) and Ovington (1957, Ovington & Madgwick 1959). Some woody communities, in climates producing a marked annual rhythm of growth, offer valuable aids to such research in the forms of wood rings and bud-scale scars by which this year's growth and past years' accumulated biomass may be distinguished. It is the purpose of this paper to discuss an approach to net primary production based on these marks of annual rhythm.

COMMUNITY SAMPLING

Two principal approaches to measurement of current growth in the field are possible (excluding for the purposes of this paper gaseous exchange and other molecular techniques)—weighing or other measurement of foliage and current twigs, and determination of wood radial increments. In sampling techniques used in the Great Smoky Mountains, a 0.1 hectare quadrat extending 10 m on each side of a 50-m steel tape is laid out and marked. All trees and arborescent shrubs in the quadrat are tallied by diameter and species from the one-inch diameter class up. Increment borings are taken for major species from a sufficient number of trees within or close by the quadrat to represent the range of size-classes, and individual trees of rarer species and largest sizes are bored. For each tree bored, radial wood increment for the past decade, bark thickness, age, height, and diameter at breast height are determined. Current foliage of undergrowth plants is clipped in 20 small (0.5 × 2 m) quadrats scattered (random numbers of meters out on each side of 5-m intervals along the tape) over the area of the larger quadrat. In each of these the herbs are clipped at ground level, shrubs at the last bud-scale scar. Per cent foliage removal by animals is recorded when this can be observed and estimated. Live weights of each species in each quadrat are determined in the field for statistical purposes; live and dry weights for each species from all 20 quadrats combined are determined in the laboratory. Since shrubs of 0.5 in. or more dbh are treated as tree stems, only those below this limit are clipped. A quadrat area greater than 0.1 ha is desirable for forests containing large trees. Shrub community samples are based on clippings from 10, 0.5 × 2.0 m quadrats scattered in the stand.

¹ This is the first publication from a project on "Productivities of plant communities in the Great Smoky Mountains," supported by funds from the National Science Foundation. Field data from the hemlock-beech cove forest were taken, and the methods described under "Community Sampling" and Production Analysis of Shrubs" developed, by the author in collaboration with R. W. Becking. The project was made possible by permission to take vegetation samples without disturbance in the Great Smoky Mountains National Park, and permission to cut trees and large shrubs for production analysis on National Forest lands outside the Park. The author is indebted to Stephen H. Spurr for comments on the manuscript.

TREE-STRATUM COMPUTATIONS

Data taken from the stand permit computation of basal areas of wood plus bark and of wood only, and bole volume if suitable volume tables are available. When they are not, a preliminary approximation of volume can be obtained from Spurr's (1952) volume equations without species corrections, or by the assumption that the bole approaches a paraboloid of rotation for which the volume

is represented by $V_p = \frac{\pi}{2} r^2 h$, in which r is the wood

radius at breast height and h is tree height. The limitations of this "parabolic volume" may be granted, but it permits comparison of stands; and on it one approach toward estimation of wood growth may be based. Basal area increment and height growth are separately estimated, according to the two-way method of Spurr (1952). Basal area increments are computed from the wood basal areas and average or individual radial increments. Height growth estimation is based on curves relating height to age for major species in the stand, and the age and height data, in relation to height curves of normal shape, for individual trees of rarer species. Given estimates of basal area increment and height growth, one may compute volume growth for each size class of major species and each individual of rarer species and largest sizes by the difference in parabolic (or otherwise determined) volumes before and after a year's growth ("parabolic volume increment"). This estimate weights heavily the height growth, as this reflects elongation of the stem or of both stem and branches. One-half basal area increment times height provides an alternative estimate of volume growth by the stem or bole itself; this value is termed here "estimated stem volume increment."

CONVERSION FACTORS

There now result two independent, part-measurements of production—estimated volume increment for trees and larger shrubs, and clipping production for smaller shrubs. These must be related to each other and to the desired community-wide measurement—net annual production, or the primary productivity, exclusive of that expended in respiration by the plants, measured as dry weight of current growth per year. For the smaller shrubs ratios are needed relating total shoot growth, and total shoot and root growth, to clipping production. For larger shrubs and trees, estimated volume increment must be related to actual volume and weight growth of bole, and to total shoot and total shoot and root growth. To determine these relations, the distribution of current production in the various major fractions of woody plants and the relation between estimated volume increment and actual growth must be studied. Ovington's (1957) approach through age-sequences of average individuals in plantations is thought inappropriate to uneven-age climax stands; methods determining production distribution for each individual studied are needed. Such methods will be described as they apply to shrubs.

PRODUCTION ANALYSIS OF SHRUBS

A shrub to be studied is felled, and stem sections or "logs" (usually 0.5 m in length) are marked off. Branches

are removed from the base upward; for each branch are recorded height above stem base, branch basal diameter, length and age, and weight and number of current twigs and leaves, of older leaves, if any, by years, and of fruits or fruit clusters. For each log are recorded basal and mid diameter, basal age, bark thickness, radial wood increment, and live and dry weight of the log or a sample disc. For some sample branches live/dry weight ratios are determined for branch wood of different ages, current twigs, leaves, separated by ages if the plant is evergreen, and fruits. For some sample logs bark is stripped off for live and dry weighing, and log surface and average bark thickness are determined. For as many individuals as possible, root systems are dug up with as much care as possible, and root live and dry weights determined. Diameters of broken roots are recorded, and basal diameter and weight are determined for enough intact roots to permit construction of curves relating average weight to basal diameter.

BRANCH AGES

Age determination of branches proves to be a special difficulty, subject to several types of errors: (a) Ages determined only from wood rings at the bases of branches are often in error by several years (cf. Reukema 1959). (b) Age determination by bud-scale rings and branching nodes is often more reliable, but these cannot be counted with confidence in older branch wood. (c) Some twigs of older, lower branches fail to form a current twig in a given year. (d) Secondary current twigs or Lammas shoots are formed during the season by vigorous upper branches in some species. (e) Although branch age will usually accord with stem age at the point of branching, development from dormant or adventitious buds occurs in a few branches of some species, and in some other species is common. Branch ages should be determined not by any single means, but by careful checking against one another of both bud-scale and wood-ring ages of both branches and logs. Reasonable confidence in branch ages is possible when the shrub is thus studied as a whole.

PRODUCTION DISTRIBUTION COMPUTATIONS

Given the preceding measurements one may determine or estimate the dry weight production of the different fractions of the shrub: (a) Clipping (current twig and leaf) production, and fruit production if any, are directly measured. (b) Older leaf growth, in evergreen species, may be estimated from the increase of average dry weight per leaf from current to older leaves, together with the total numbers and weights of older leaves by years. If the greater average weight of older leaves results in part from loss of smaller leaves, such estimates will be in error; but counts of leaves of different ages may give some assurance that apparent growth does not result from loss of smaller leaves. (c) Stem wood growth may be determined from the ratio of the cross-section area increase for the current year to the cross-section area of the wood, times the wood dry weight for the log. It has not been thought feasible to separate sap- and heartwood in shrubs. To allow for curved taper, cross-section areas should be based on the mid point of the log, or the average of cross-section areas, not of diameters, for the ends of the log (Huber and Sralian formulas). (d) Relative bark thickness increase at different ages can be estimated from curves of bark thickness in relation to age, although sloughing from the surface of older bark cannot be adequately allowed for. Bark growth for a log can be estimated from relative bark thickness increase as related to log age, wood growth of the log as it increases bark surface area, and dry weight of bark present, whether

measured or estimated from bark thickness and surface area. (e) Growth of branches (wood and bark together, excluding current twigs) is very difficult to measure directly. Estimation has been based on construction of curves of branch weights in relation to age, with the branch population stratified by relative vigor of growth, as indicated by weight in relation to age or current twig and foliage weight. Average rates of branch weight increase/branch weight at different ages may thus be determined, and branch dry weights multiplied by these rates. Rates of growth differ widely in different branches of the same shrub, and a production estimate for a single branch may be substantially in error. Combining such estimates for all branches may give a reasonable value for branch growth, though a value which is necessarily an estimate, not a measurement. (f) Root growth also is inaccessible to direct measurement. Estimation of root production has been based on curves of total root weights in relation to total woody shoot weights at different ages, and on the assumption that the ratio of root and woody shoot growth approximates the ratio of root and woody shoot biomass. Roots, like twigs and branches, die and are lost during the life of the plant; and the magnitude of this loss cannot be accurately determined.

RESULTS—PRODUCTION RELATIONS OF *Rhododendron maximum*

Table I summarizes biomass and production distribution, with and without roots, for *R. maximum* in a hemlock-beech ravine cove forest, 1400 ft. elev., Laurel Hollow, Cherokee National Forest, Great Smoky Mountains, Tennessee. Data are based on sets of 10 older (20-50 years) and more vigorously growing "dominant" individuals, 10 smaller (12-25 years), less vigorously growing "intermediate" or "suppressed" individuals, and 10 younger (9-13 years) small and mostly unbranched plants. Other ratios needed for production estimation are given for "dominant" individuals in Table II. Regression lines, to which correspond high coefficients of correlation, have been computed for some of these values; but presentation in the form of ratios with standard errors of means for sets of 10 individuals has been preferred here. Since the values given are independently computed averages of sets of 10 ratios, they will check against one another approximately, not exactly. Standard errors of means for 10 measurements of total production/clipping production are of the order of 4 to 5% for *R. maximum* and other shrub species studied. Because of differences in branch pattern and relations of radial increment to height, and for other reasons, estimates based on volume increment are subject to wider errors; standard errors of means for ratios of total production to estimated volume increment are of the order of 8 to 10%. Root/shoot ratios are widely variable with age and from individual to individual for a given age. Ratios for total root dry weights to total stem and branch wood and bark dry weights, with estimates of dead root and branch weights from basal diameters, were 2.51 for seedlings of 3-7 years, 1.78 and 1.24 for small shrubs, 10-13 and 13-17 years, and 0.75 for medium-sized shrubs, 14-25 years. Root/shoot ratios of individuals among the latter set varied from 0.36 to 1.12, with a standard deviation of ± 0.23 .

APPLICATION—SPECIES AND STAND PRODUCTION

From these ratios the net annual production by *R. maximum* in this stand may be estimated. Clipping dry weight for smaller individuals was 2.6 g/m² indicating, with the ratios for intermediate shrubs, 6.5 g/m²/yr of shoot and 9.0 g/m²/yr of shoot and root production. Estimated stem volume increment for a population of

TABLE I. Biomass and production distribution for *Rhododendron maximum* in a hemlock-beech cove forest. All values are based on averages of 10 shrubs except root data for dominant shrubs, based on 5 shrubs.

PERCENTAGES IN—								Biomass Accumulation Ratio	Total production Clipping dry weight
	Stem wood	Stem bark	Branches	Old leaves	Fruit	Current twigs	Roots		
BIOMASS									
Dominant									
Shoot only	44.1	3.9	31.1	16.7	.2	4.0	—	8.9	—
Shoot & root	28.9	2.6	20.4	11.0	.1	2.6	34.4	—	—
Intermediate									
Shoot only	48.3	4.0	15.1	26.4	—	6.2	—	5.6	—
Shoot & root	32.8	2.7	10.2	17.9	—	4.2	32.2	—	—
Small									
Shoot only	16.4	6.4	3.8	59.2	—	14.2	—	4.1	—
Shoot & root	11.3	4.4	2.6	41.0	—	9.8	30.9	—	—
PRODUCTION									
Dominant									
Shoot only	24.2	2.7	22.1	15.7	1.6	33.7	—	—	3.00 ± .11
Shoot & root	17.8	2.0	16.3	10.5	1.2	24.8	27.4	—	3.99 ± .16
Intermediate									
Shoot only	34.5	4.2	10.2	13.1	—	38.0	—	—	2.58 ± .18
Shoot & root	25.6	3.1	7.6	9.7	—	28.2	25.7	—	3.47 ± .17
Small									
Shoot only	11.0	4.7	2.7	22.8	—	58.8	—	—	1.66 ± .04
Shoot & root	8.6	3.7	2.1	17.8	—	45.9	21.9	—	2.16 ± .09

TABLE II. Average production interrelations for "dominant" *Rhododendron maximum* in a hemlock-beech cove forest, with standard errors of means for sets of 10 measurements

	Shoot Only	Shoot & Root
Total production, g dry weight	2.39 ± .18	3.29
Estimated stem volume increment, cm ³		
Total production	3.67 ± .34	5.06
Stem wood production		
Total production, g dry weight	1.96 ± .08	
Parabolic volume increment, cm ³		
Total production, g dry weight	73	101
Leaf blade area, m ²		
Stem wood production, g dry weight	0.667 ± .039	
Estimated stem volume increment, cm ³		
Clipping production, g dry weight	0.82 ± .085	
Estimated stem volume increment, cm ³		
Clipping production	1.28 ± .16	
Stem wood production		
Actual wood volume increment	1.14 ± .06	
Estimated stem volume increment		
Actual stem wood volume	.995 ± .050	
Parabolic estimate of wood volume		
Wood specific gravity, dry g/cm ³	.615	
Leaf blade area, cm ²	76.4	
Blade & petiole dry wt., g		

production, 242 g/m²/yr total shoot and root production, and 0.42 and 1.96 m²/m² of current and older leaf surface in relation to ground surface on which this production is based. These values may be compared with those for all species together in a shrub community of a mixed heath bald on a north-facing slope of Brushy Mountain, 4900 ft elevation, Great Smoky Mountains National Park, Tennessee: 266 g/m² current twig and leaf production, 572 g/m²/yr total shoot production, about 1000 g/m²/yr shoot and root production, and 1.69 and 2.29 m²/m² of current and older leaf surface in relation to ground surface. Herb growth is sparse; and herb production less than 1% of the total, in both stands. Consumption of current shrub foliage by animals also is small in both cases, and the measured net growth should closely approach net annual production.

PRODUCTION AND BIOMASS DISTRIBUTION IN THE COMMUNITY

Such data permit a number of other approaches to community structure and characterization, among them: (a) The biomass/production or "biomass accumulation ratio," the ratio of the total dry weight of living plants, or other appropriate biomass measurement, to net annual production, may be determined. The ratio is thought to be an ecologically significant variable ranging downward from large, old-growth forests to 1.0 in some herb communities and less than 1.0 in plankton. Ratios estimated from stem sizes and numbers in the stands discussed are 10.0 for *R. maximum* only in the cove forest and 4.7 for the shrubs of the mixed heath bald. (b) A perennial problem of plant synecology is the ranking of species of different growth forms and statures, for which the "importance value" (Curtis & McIntosh 1951) and other measures are used. Production seems the best single dimension by which species may be ranked according to functional significance in the community; for some purposes biomass, or such particular expressions of production as clipping dry weight or volume increment may be appropriate. Ranked by estimated volume increment, *R. maximum* is the third most important species, after *Tsuga canadensis* and *Fagus grandifolia*, in the cove forest stand. These three species

2510 larger stems per hectare was 0.736 m³/ha (73.6 cm³/m², 10.5 ft³/acre). Application of the ratios to these values yields for arborescent *Rhododendron*: 60 g/m² current twig and leaf production, 176 g/m²/yr total shoot

share "production dominance" in the stand. The shrubs of the mixed heath bald rank by clipping dry weight in the order—*Rhododendron catawbiense* 162, *Kalmia latifolia* 76, *Viburnum cassinoides* 9, *Vaccinium constablaei* 9, *Gaylussacia baccata* 6, and *Pyrus melanocarpa* 4 g/m². (c) Ranking of species in this manner permits approaches to relative dominance and species diversity which are independent of area relations and assumptions about "individual" plants. Of the various diversity measurements (Hairston 1959), two of the simplest may be applied to the data—Simpsons (1948) index of concentration of

dominance, $\alpha = \sum \left(\frac{x}{n}\right)^2$ (in which x is an individual spe-

cies production measurement, and n is the total production for all species), and the slope r for a geometric progression, $x = ar^{(n-1)}$ (in which a is the production measurement for the first species and n the number of a species when all species are arranged in sequence from highest production to lowest, with least squares fit for r). For the cove forest and heath bald these values become—, $\alpha = 0.208$, 0.455 , and $r = 0.683$, 0.477 —expressing the greater species-diversity of the cove forest, the greater concentration of production dominance in a few species in the heath bald.

SUMMARY-CONCLUSION

Measurement of production in forest and shrub communities may always be difficult, but it is by no means impossible. In climates with strong seasonal fluctuations, the marking of the current year's growth by wood rings and bud-scale scars makes possible effective estimation of net primary production by woody plants. Steps in the approach to such estimation described are: (a) field measurement of community production by clipping current twigs and leaves of smaller shrubs, and stand counts of larger shrubs and trees together with increment borings and height determinations, (b) computation, for trees, of estimated volume increment, (c) analysis of major spe-

cies to determine production ratios (total production to clipping production, and stem wood and total production to estimated volume increment), and (d) estimation of net production by woody plants in the community from the field measurements times the correction ratios to total production. The resulting data also permit effective approaches to species ranking, relative dominance and species diversity, and other aspects of community analysis and characterization. The techniques described here may be subject to substantial improvement; they are offered not as a perfected method but as a direction of research. Analysis of production and volume relations of trees is laborious, but such research will have to be carried out by ecologists and foresters if the method is to be applied to the productivity of forests.

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PHYTOPLANKTON FROM PYMATUNING RESERVOIR IN DOWNSTREAM AREAS OF THE SHENANGO RIVER¹

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The increased number of flood-control, navigational, and dual purpose dams constructed on rivers and streams in recent years has resulted in many physical and biological changes, not only within the confines of the impoundment, but for some distances downstream. Of considerable interest to the biologist are the phytoplanktonic organisms discharged into rivers from highly productive reservoirs. It is important to understand the changes which occur in algal communities of lentic origin when they become part of a lotic situation. Knowledge of how far below a reservoir the concentration of algae remains high is of interest, particularly when cities downstream depend on the river for water for domestic or industrial use.

Kofoid (1903, 1908) pointed out the importance of impoundments and backwater areas as sources of abundant plankton crops in the Illinois River. That plankton populations of impoundments were richer than those in the

river was also reported by Galstoff (1924). Damann (1951) investigated this in a study of the Missouri River and its tributaries. Here plankton productivity in reservoirs was considerably less than in streams or rivers below reservoirs. This he considered a result of a clarification and nutrient enrichment brought about by the use of the reservoir. Chandler (1937, 1939) studied the movement of plankton from lakes into small drainage streams. A rapid decrease in plankton populations was observed with downstream distances as a result of the filtering action of aquatic vegetation. Reif (1939) similarly studied the effect of stream conditions on lake plankton but reported little quantitative data.

The present study was concerned with changes in quantity and species-composition of phytoplankton from Pymatuning Reservoir as it moved about 10 miles down the Shenango River. This combination of river and reservoir in northwestern Pennsylvania is particularly well suited for this study. The river begins at the outlet

¹ Pymatuning Laboratory Publication No. 21.

of the reservoir and for most of the distance investigated, receives proportionately little water from tributaries. Furthermore, the high productivity of the impoundment (Tryon and Jackson 1952, Hartman and Graffius 1960) insures a high initial phytoplankton population in the river. The investigation was carried out during the 3 summer months of 1956 when the concentration of algae in the reservoir was high.

METHODS AND PROCEDURES

Six collecting stations were located at intervals with convenient access for sampling within the impoundment and along the upper course of the river (Fig. 1). Station 1 was within the impoundment, just above the dam. Station 2 was in the raceway of the outlet of the dam, just below the gates. Stations 3, 4, 5, and 6 were at bridges crossing the river at intervals of 1.55, 3.80, 6.80, and 10.57 miles downstream from the dam.

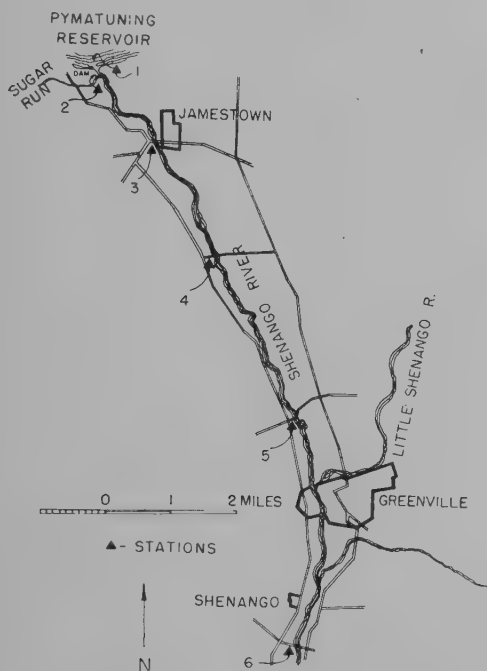


FIG. 1. Map of upper reaches of the Shenango River showing locations of the six collecting stations.

Within the limits investigated, the Shenango River is a fast-flowing stream about 90 ft. wide and as much as 7 ft. deep in the deeper parts. The region through which it flows is primarily agricultural and for more than half of the distance studied the river bank is lined with trees. Where the river flows through heavily wooded areas, a few fallen trees or debris sometimes partially block the channel, but in general, there are not many slow or shallow riffle areas. There is almost no submerged vascular vegetation in the river bed except where a small dam just below the mouth of the Little Shenango River in Greenville creates a small impoundment. Here the current is slow, and patches of *Nuphar advena* grow in shallow areas.

Eleven sets of water samples were taken from each station at 7 day intervals from June 15, 1956 to August

27, 1956. Four liters of water were collected at each sampling period, 3 for gravimetric determination of suspended materials and one for counts of algal organisms. For determinations of suspended organic and ash material, triplicate liter samples were centrifuged in a standard Foerst Electrical Centrifuge for 6 to 7 min. Residue from the centrifuge cup was dried in tared silicon crucibles, weighed, and ashed in a muffle furnace. Calculations of total weight, organic (weight lost by ignition), and ash weight for the liter samples were thus obtained. Counts of phytoplankton organisms were made using a Sedgwick-Rafter counting chamber and Whipple ocular, following standard procedures. Counts were recorded as number of cells for single-celled forms and number of colonies for colonial forms. These values were converted to total number of cells by multiplying recorded values by conversion factors (Hartman and Graffius 1960).

RESULTS

During this study, 36 genera of planktonic algae were common in the reservoir and river. Through the summer, with the exception of collection 1 which had relatively high percentages of Chlorophyta, the phytoplankton community was dominated by the Cyanophyta. Dominant species during this period were: *Microcystis aeruginosa* Kuetz.; *emend* Elenkin, *Coelosphaerium Naegelianum* Unger, *Aphanizomenon flos-aquae* (L.) Ralfs, *Anabaena circinalis* Rabenhorst, and *Anabaena spiroides* var. *crassa* Lemmermann. For most of the summer these comprised more than 90% of the phytoplankton community. Chlorophyta, particularly *Pediastrum Boryanum* (Turp.) Meneghini, *Scenedesmus quadricauda* (Turp.) de Brébisson, *Coelastrum microporum* Naegeli, *Sphaerocystis Schroeteri* Chodat, *Planktosphaeria gelatinosa* G. M. Smith, *Pandorina morum* (Muell.) Bory, and *Oocystis* sp., made up about 8%, and other groups, chiefly Chrysophyta, comprised the remainder.

Quantitative results of analyses from 5 of the weekly collections for the 6 sampling stations are presented graphically in Figure 2. These are representative of the data obtained over the entire period of the study. Total number of cells determined by actual counts ranged from a low of 31.7×10^6 for Station 6 on July 16, 1956 to a high of 307.1×10^6 for Station 1 on August 27, 1956. From July 30 to the end of the investigation (collections 7 to 11), the concentration of cells was greater than during the first 6 weeks of collecting. The number of cells per liter for each collection period followed a general pattern at successive downstream stations. A slight decrease was commonly observed between Station 1 in the reservoir and Station 2 in the outlet raceway. This was followed by an increase at Station 3 and then a decrease at each succeeding downstream station.

Gravimetric determinations were discontinued after the sixth collecting period when it became apparent that weights of suspended organic material did not correlate with cell counts of phytoplankton. In all cases, weight of the organic and inorganic (ash) fraction of the suspended substances increased with distance downstream. Gravimetric values from collection 4 on July 9 showed the greatest increase in weight, with the organic fraction increasing from 4.2 mg to 15.3 mg and the ash fraction from 5.9 mg to 90.1 mg between Stations 2 and 6. These changes were obviously the result of silt carried into the river by run-off waters. Throughout the study the Shenango River was unusually high and turbid because of abnormally high rainfall over the watershed during the 3 summer months. Precipitation for this period, measured at the Department of Forest and Waters office at the Pymatuning Dam, was 8.01 in. above the 44 yr average

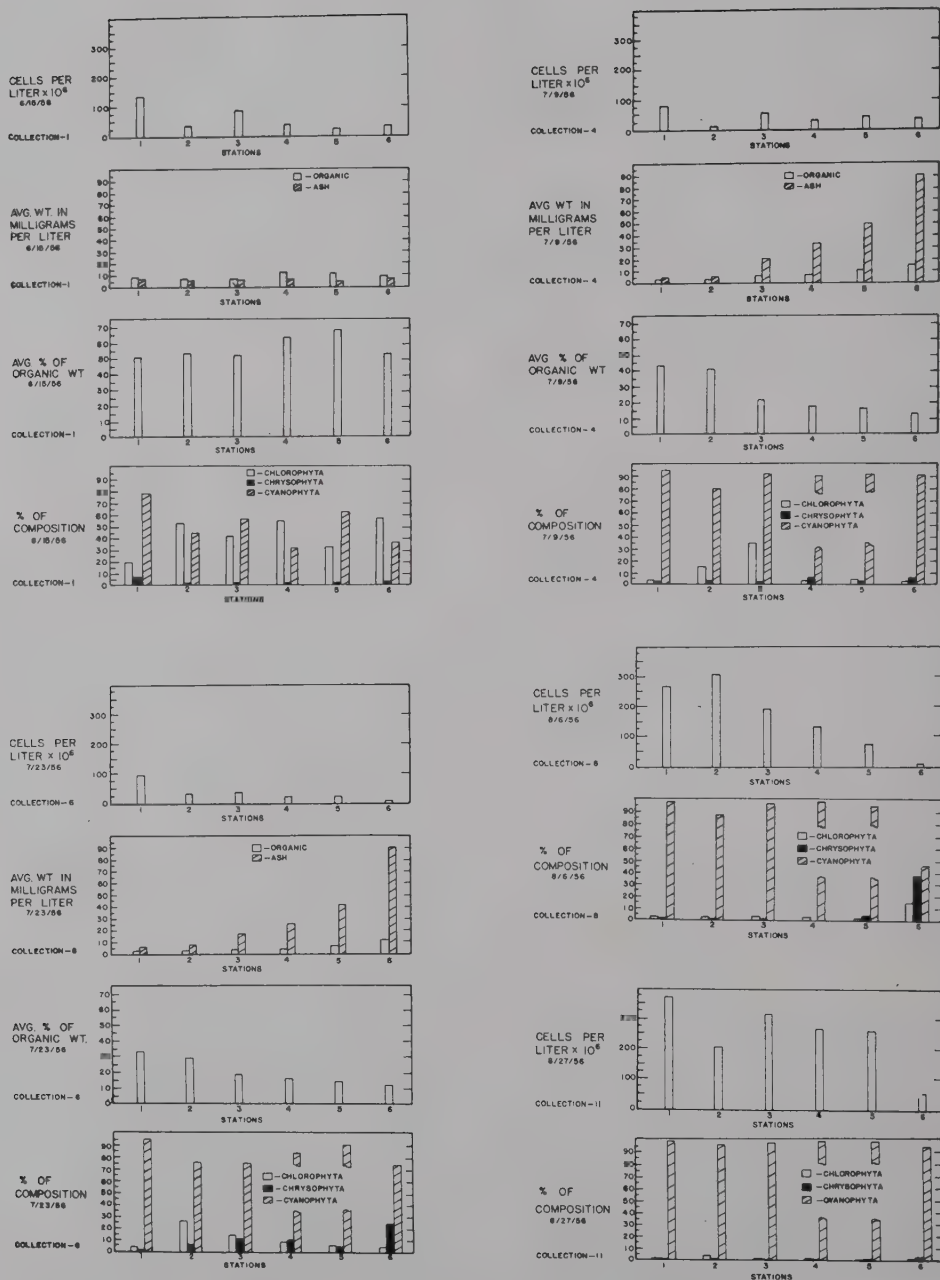


FIG. 2. Representative results of phytoplankton collections from the Pymatuning Reservoir and sampling stations in the Shenango River.

with an excess of 2.98 in. in June, 2.09 in. in July, and 2.94 in. in August.

That increased weight of suspended material in the river did not represent an increase in phytoplankton is indicated by the fact that the percentage of organic weight in the sample usually decreased with downstream stations (Fig. 2). For example, in collection 4 on July 9 the percentage of organic material decreased from 42% to 14% between Stations 2 and 6.

DISCUSSION

The species composition of the phytoplankton communities at upstream stations in the Shenango River is quite similar to the community structure in the Pymatuning Reservoir. This is not surprising, since in the upper reaches of the river covered in this study, the greater amount of water is derived directly from the reservoir. The few small tributaries and surface run-off contribute little plankton to the river. Qualitative or quantitative changes observed in the phytoplankton between stations are therefore a result of dilution, currents, and turbidity, or other ecological conditions of the river.

The consistent decrease in numbers of organisms between Station 1 in the reservoir and Station 2 deserves comment. Gate opening at the dam drain water from 15 to 20 ft. beneath the reservoir surface. This water is released with great force through two narrow raceways resulting in considerable turbulence and a rapid current. Although the vertical distribution of phytoplankton in the reservoir is fairly uniform, water from beneath the surface would be expected to show a somewhat lower concentration of algae than surface samples, particularly when colonial blue-green species dominate the community. The difference in total number of organisms at Station 2 is not a result of dilution by tributary waters since the collecting station was in the raceway of the dam. Mechanical damage and destruction of colonial forms may be important here.

The increase in organisms at Station 3, although not entirely consistent during the study, might be explained by the fact that water released from the reservoir is soon slowed by the broad river bed with its many meanders. This gives the phytoplankton an opportunity to utilize the available nutrient materials. Damann (1951) found that phytoplankton increased below many of the reservoirs in the Missouri River and he correlated this with enrichment of the downstream areas. It should be noted that Sugar Run enters the Shenango River just below Station 2 and may supply additional nutrients. Decrease in population at successive downstream stations may be a result of nutrient depletion or of mechanical destruction in riffles and rapids. The high silt content and turbid conditions during much of the collecting period probably also were important in decreasing the number of organisms (Ellis 1936).

Chandler (1937), in a study of two rivers, showed a decrease in phytoplankton of 70% within a distance of 20 m in one and a decrease of 60% within 15 m in the other. Both streams were heavily vegetated with submerged aquatics and the filtering action of these plants was accorded prominence as a cause of the decrease. In the Shenango River there is almost no submerged vegetation and filtering was not an important factor. During the collecting period, the average decrease in total numbers of cells from Station 1 to Station 6, a distance of 10.57 miles, was 72.6%.

A significant change in community structure with downstream distance was the increase in percentage of the Chrysophyta. Although the blue-green species, abundant in the reservoir during the summer, remained dominant at all downstream stations, the proportion of dia-

toms often increased. This was particularly evident at Station 6. This change in community composition apparently resulted from the addition to the phytoplankton of benthic diatoms developed in Shenango and its major tributaries. Little Shenango River which enters above Station 6 (Fig. 1) no doubt contributed heavily to this situation.

This study indicates that productive impoundments particularly may greatly affect conditions in rivers for considerable distances below the impoundment. High phytoplankton populations and their accompanying biological, chemical, and physical effects create new problems for water plant operators, public health officials, sanitary engineers, and all who are concerned with the use of such waters. There is the need for consideration and appraisal of the creation of such conditions when planning for construction of new impoundments.

SUMMARY

1. The effect of phytoplankton from highly productive Pymatuning Reservoir on its drainage outlet, the Shenango River, was studied during the summer at 6 collecting stations covering a downstream distance of 10.57 miles.
2. The phytoplankton of the upper Shenango River is typical of that found in the Pymatuning Reservoir.
3. An average decrease in numbers of cells of 72.6% was found between the reservoir and the last collecting station.
4. The proportion of diatoms in the community generally increased at downstream stations.
5. Rapid current and high silt content of the river were considered important factors in decrease in numbers of organisms.
6. Phytoplankton from Pymatuning Reservoir exists in downstream areas in high enough concentrations to suggest potential problems for water users. There is need for consideration and appraisal of the creation of such conditions prior to the construction of new impoundments.

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ECOLOGICAL RELATIONSHIPS AND ECONOMIC IMPORTANCE OF JAPANESE MICROTINAE

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Voles are discontinuously distributed throughout the 4 main islands in Japan, and provide a chance to study their varying habitats under different ecological conditions. This topic has been discussed for several areas in Japan by Tokuda (1950) and Ota (1955 and 1958), whose works point out that the habitat of a given species or genus varies from one island to another. In a country where agriculture and forestry are major activities, environmental distribution of voles has a great economic importance. Under certain conditions, species in each of 3 genera of microtine rodents have done severe damage to young pines, larch, cypress, and cedars; and on each of the 4 large islands, poison campaigns and habitat manipulation have been conducted to suppress sudden increases of one or another of these little rodents. It is the practice of Japanese foresters to log large blocks at a time, and shortly after the trees are removed the ground is covered by a dense growth of grasses and forbs. Such cover is soon inhabited by one or another species of vole. Herbaceous cover is cut several times a year and this tends to destroy the habitat of voles. With spring rains and strong sunlight, grasses and forbs may flourish; if these are not cut, voles may increase. Vole populations have increased suddenly in unmanipulated areas.

GENUS *Clethrionomys* TILESUS

There are 4 species of *Clethrionomys* in Japan. *C. rutilus*, a small, brightly-colored species, occurs only in Hokkaido and is found throughout the island. Although it lives in a variety of habitats, it is usually rather uncommon and not of great economic importance.

Clethrionomys rufocanus, a larger, darker form with shorter fur, is far more abundant than *C. rutilus* on Hokkaido. The subspecies *C. rufocanus bedfordiae* occurs throughout Hokkaido. The closely allied *C. andersoni*, on northern Honshu, lives southwest to Nagano-ken in the high mountain forests. In extreme southern Honshu, at lower elevations in Wakayama-ken there is a rather brightly-colored species of *Clethrionomys* which could possibly be a relict from an earlier movement of *rufocanus* (or a relative) into Honshu. This recently discovered (and unnamed) form may have previously been confused with *Eothenomys smithii*.

GENUS *Eothenomys* MILLER

The small red vole called *smithii* has been placed in several genera by different workers and its correct relationship may be established only by a study of long series of the several species both from the eastern Asiatic mainland and from the adjacent islands. Tokuda (1955) pointed out the relationship between *smithii* of Japan and species of *Antelomys* of the Chinese Province of Yunnan, and for this reason placed *smithii* in *Antelomys*. There is no evidence to contradict Tokuda's excellent discussion but, following current generic concepts, we consider *Antelomys* to be a synonym or a subgenus of *Eothenomys*. *Eothenomys* is represented on Shikoku, Kyushu, and Honshu, but does not occur on Hokkaido. *E. smithii* is a common species on Honshu, Shikoku, and Kyushu, and

a little known subspecies, *E. s. okiensis* Tokuda occurs on the Island of Oki in the Sea of Japan. *E. kageus* Imaizumi (1957) was described from the northeastern half of Honshu. *E. kageus* closely resembles *E. smithii*, and may indeed be a subspecies or a local form of *smithii*; the two forms appear to be ecologically comparable.

GENUS *Microtus* SHRENK

Microtus montebelli is the only Japanese representative of its genus, and is found only on Kyushu and Honshu. It is a yellowish black species of microtine rodent, and is not likely to be confused with any russet-colored species of *Clethrionomys* or *Eothenomys* in Japan.

COMMENTS

Because the habitat of a given genus of vole depends, in part at least, upon the presence or absence of other voles, each island is discussed separately. Because the actual physical and psychological relationship of these 3 genera are so poorly known, we cannot begin to discuss the elusive role of competition; and it is difficult to determine, without detailed biological field studies of these rodents, the object for which they compete. Simply from their different environmental distribution on the 4 islands, it is rather obvious that these voles do compete with one another, or are incompatible.

On Hokkaido *Clethrionomys rutilus* and *C. rufocanus* are the only voles; an interesting feature of the rodent fauna in Hokkaido is the absence of a species of *Microtus*. *C. rufocanus* typically is far more abundant and widespread than the smaller *C. rutilus*. Like various species of *Clethrionomys* throughout Eurasia and North America, *C. rufocanus* is a common inhabitant of wooded and forested areas, but unlike red-back voles in other regions, *C. rufocanus* in Hokkaido is a typical rodent of grassy meadows and open hillsides where the cover is mostly herbaceous (Ota 1955, 1956). *C. rufocanus* does not create clearly apparent surface runways that are characteristic of most species of *Microtus*, but careful examination of suitable habitat usually discloses less well developed paths through grass, and piles of scats and cut stems of grasses and forbs indicate microtine activity. On the shore by the Sea of Okhotsk, near the city of Abashiri, we found *C. rufocanus* to be very common, and trapped them both on the grass and rose-covered sand dunes, a few meters from the water, and in an adjacent low-lying pasture of rose bushes, grasses, iris, and forbs. Rose hips (*Rosa rugosa*) were ripe and in late August were the main food for these voles. They ate mostly the soft flesh and discarded skins and seeds were everywhere on the ground. There were no fallen fruits so these voles must have climbed bushes for their food. In this particular area the only other common mammals were 2 shrews, *Sorex shinto* and *S. unguiculatus*.

As *C. rufocanus* is so frequently encountered in open herbaceous cover in Hokkaido, it commonly occurs in plantations of young conifers, especially of larch (*Larix kaempferi*). When the numbers increase, this vole often girdles tender trunks of young trees, and sometimes from 50 to 90% of a plantation is so destroyed. This danger requires constant care on the part of the Ministry of Agriculture and Forestry, which employs especially trained biologists whose duty it is to detect and control outbreaks of voles before excessive damage occurs. From the sylvicultural aspect, *Clethrionomys rufocanus* is the

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most important rodent in Hokkaido. In conifer plantations where it is most likely to be destructive, wood mice (*Apodemus speciosus* and *A. geisha*) are scarce or absent.

On Honshu the Microtinae is represented by 5 species in 3 genera. *Clethrionomys andersoni* inhabits forests of fir (*Abies* spp.) and spruce (*Picea* spp.) from Aomori-ken, south at progressively higher elevations, to the Southern Japan Alps in Nagano-ken where it lives at 2000 meters and above. Although *C. andersoni* may sometimes be found in thickets of *Ribes* spp. and *Rubus* spp., it does not occupy open grassland and it has not invaded plantations of young conifers. The habitat of *C. andersoni* precludes it from being of any great agricultural or sylvicultural importance. The other representative of the genus *Clethrionomys* is the unnamed form in low-elevation broad-leaved forests and rocky slopes in extreme southern Wakayama-ken, the southernmost part of Honshu.

Eothenomys smithii replaces *C. andersoni* in southwestern Honshu, and *E. kageus* extends at lower elevations north to Iwate-ken. On Honshu, these voles are forest-dwelling species, and do not occur in grasslands. *E. smithii* (or *E. kageus*) is especially common and lives at elevations of at least 1600 meters in regions where *C. andersoni* occurs, and may be found to the tree limit in regions where *C. andersoni* is absent as, for example, on Mt. Fuji. *E. smithii* inhabits wooded areas at least as low as 100 meters, but does not seem to invade exposed grasslands, and, on Honshu, is not known to be a species of any economic significance.

In contrast to the 2 above species, *Microtus montebelli* is a characteristic inhabitant of grassy and herbaceous cover, and may be sporadically abundant in the grassy valleys (as in Akita-ken and Niigata-ken) and open forb-covered hills of Honshu. It occurs from sea level at least up to 1600 and 1800 meters elevation. In these situations, *M. montebelli* treads its characteristic trails through the grass, and at times has girdled and killed large numbers of young (2 to 4 year old) Japanese cedars (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*). These trees are important timber species on Honshu, and seem quite susceptible to the attacks of *M. montebelli*. An outbreak of *M. montebelli* usually results in high mortality of young cedars, cypresses, and pines, and this rodent seems to be the only vole involved in such damage on Honshu. In these open areas *Apodemus* spp. are quite uncommon and of no economic importance.

¹On Kyushu, *E. smithii* and *M. montebelli* are the only voles present (Hiraiwa *et al.* 1957), and, for the most part, the 2 species are inhabitants of woodlands and grasslands, respectively. Moreover, on Kyushu, *E. smithii* is more abundant at higher elevations, especially above 500 meters. *M. montebelli* lives from sea level to the upper slopes (1600 meters) of Mt. Kuju, the highest peak on Kyushu. It is the only mouse on Kyushu that has been found to cause damage in plantations of young pines and cedars. In these planted areas, the spring rains and strong sunlight cause grasses and forbs to flourish, and the environment is suitable for sudden increases in vole populations. On Kyushu there have been occasional outbreaks of *M. montebelli*, and on occasion this species may destroy a large number of young pine trees. In early 1958 in Kumamoto-ken in central Kyushu, *M. montebelli* increased on the grassy slopes where they girdled and killed up to 90% or more of the young pines. *E. smithii* was not found in pine plantations in Kyushu, and is not believed to be of economic significance on this island.

On Shikoku, the smallest of the 4 main islands, the only microtine rodent is *Eothenomys smithii*. Although this vole is more abundant at higher elevations on Shikoku,

it lives alike in forests and on grassy slopes. As open areas are frequently potential forest lands and of little agricultural value, they are usually planted with young conifers. At periods of high populations, this little vole is extremely destructive and is the object of extensive poisoning operations (Tanaka 1957).

In Japan the presence of *Microtus montebelli* seems to be the key factor in determining the habitat to be occupied by the red-backed voles. On Hokkaido where there is no species of *Microtus*, the red-backed vole, *Clethrionomys rufocanus*, is usually a common dweller of grasslands, and on Shikoku where the genus *Microtus* is not known to occur, the red-backed vole *Eothenomys smithii* may be abundant in the open, herb-covered hillside. On both Hokkaido and Shikoku, *C. rufocanus* and *E. smithii*, respectively, live in forested areas also. On Honshu *M. montebelli* is rather common in undisturbed grasslands and on this island both *C. andersoni* and *E. smithii* are found only in forests. Similarly, on Kyushu *M. montebelli* occurs, and the red-back vole, *E. smithii*, is more or less confined to wooded habitats.

A comparable situation was reported by Bernard (1953). In Belgium, *Microtus arvalis* was found on cultivated land and *M. agrestis* lived on nearly fallow areas and in woodlands. Findley (1954), discussing the environmental occurrence of *Microtus pennsylvanicus*, *M. ochrogaster*, and *M. montanus* in Wyoming, noted, that these voles are ecologically separated where their geographic ranges overlap. He suggested that interspecific-competition limits the environmental distribution of these voles because in regions where any of the 3 species occurs alone, it inhabits a greater variety of habitats.

SUMMARY

The environmental distribution and economic importance of Japanese Microtinae vary among the 4 main islands and indicate that ecologic distributions of these voles depend not only upon climatic, edaphic, and vegetational features, but also upon the presence or absence of allied, and presumably competing forms. It seems most realistic to consider that, for a species of small mammal, other closely related forms may be important features of the habitat, and these associates may be as important as, or more important than, the character of the soil and vegetation in affecting habitat occurrence. This suggests that these voles do not settle in a given habitat only by choice or because of any delicate adjusted combination of adaptations, but that one species occupies more desirable environments, and an allied form takes what is left over.

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POPULATION DENSITY OF THE UNDERGROUND ANT, *LASIUS FLAVUS*,
AS DETERMINED BY TAGGING WITH P^{32}

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Lasius flavus, a yellow ant common on the calcareous grasslands near Oxford, England, has been the object of an intensive study by the junior author (Pontin 1958). These ants, which normally do not venture above ground, obtain their food by tending root aphids of several species; both honeydew and the aphids are consumed (Pontin, 1958a). Each colony maintains at or near the center of its feeding territory a conspicuous mound containing the nursery galleries. Queens are produced during the summer and their number could easily be determined by collecting them at intervals from the uppermost galleries where they remain for some time before emerging. However, estimating the number of workers presented a more difficult problem. Attempts to determine density by digging out colonies or by marking individuals with dyes proved entirely unsatisfactory. From general observation it appeared that the number of queens produced per season per colony was a good index to the size of the colony. However, until satisfactory estimates of worker density could be obtained the relationship between total density and queen production could not be determined for certain.

While in residence at Oxford University during the summer of 1958 the senior author suggested that the problem might be solved by tagging large numbers of individuals with a radioactive tracer and employing a marking-recapture method for estimating density. The colonies of *Lasius flavus* appeared to be ideal for such a technic. When flat stones are placed on top of the mounds, the ants construct extensive galleries directly under the stone where warmth from the sun is favorable for the development of the pupae. During the summer the workers move through these chambers in a continuous stream to and from the underground tunnels leading to the aphids clustered on roots of nearby plants. Large numbers of individuals can thus be removed for tagging by gently lifting the stone, and then conveniently returned to the mound with a minimum of disturbance of the colony. A simple procedure involving a single massive tagging and one or two recapture samples was indicated since individual workers of this species are all alike (and presumably behave alike), and are relatively long-lived. Individuals newly emerged from the pupae can be recognized

by their lighter color, and thereby eliminated in the tagging and recapture counts. Previous observation, as well as the results of this study, indicated that there was little or no movement of individuals from one colony to another.

METHODS

The experiments in "radio-tagging" were carried out on a patch of ungrazed grassland known locally as the "Bowling alley" located in Wytham Woods near Oxford. Stones had already been placed on many mounds in previous years. The number and distribution of colonies had remained roughly the same for the previous 2 years indicating a relatively stable population. Radioactive phosphorus (P^{32}) was employed since this isotope may be safely used in the field and when applied externally is known to be absorbed and retained for some days by insects.

Before the field experiments were begun a series of tests were made in the laboratory. In these experiments 10 to 20 ants were soaked in P^{32} solution and placed in small jars with about 50 untagged ants. A small section of one antenna of each tagged individual was clipped off to facilitate later recognition. The jars were provided with plaster-of-paris bottoms and sufficient soil to maintain a moist atmosphere similar to that of the natural habitat. At intervals of 2, 4 and 6 days ants were removed from the jars and tested for radioactivity. In all cases it was easily possible, on the basis of radioactivity, to distinguish the ants which had been dipped and those which had not. In some cases untagged ants picked up a small amount of radioactivity, presumably by ingestion of feces or fluids excreted by tagged ants. However, the difference between this "secondary tagging" and the "primary tagging" was so great that there never was any doubt as to which individuals had received the primary tag. Virtually no mortality of either tagged or untagged ants kept for a few days in the jars was observed. It was found that approximately 200 microcuries of carrier-free P^{32} in 200-300 milliliters of water provided a solution sufficient to tag hundreds of ants at a level of activity allowing detection for at least 10 days. In using this technic with other species of ants and with insects in general it would be well to point out that adding a very small amount of detergent to the solution may be necessary to obtain rapid penetration of the cuticle by the isotope; too much detergent, of course, can result in rapid "drowning" of the insects. For the "thin-skinned" *Lasius* no

¹ This study is a phase of radio-ecological investigations supported by an AEC grant (Contract AT(07-2)-10), and was carried out while the senior author held a National Science Foundation Senior Post-doctoral Fellowship.

wetting agent was needed. Finally, it is important that the pH of the solution be kept below 7.

For the mass tagging in the field a simple "dipping devise" was constructed. A straight-sided plastic cup with a fine screen wire bottom was fabricated so that it would fit snugly inside of a wide-mouth jar 3 or 4 inches in diameter. The cup was fitted with a small handle so that it could be raised and lowered in the jar, or removed from the jar. With the cup in place solution was poured into the jar so that the level was about an inch above the bottom of the cup. The top of the jar was then screwed on and the jar placed in a metal can for transportation to the field. In the field ants were aspirated from the hill into shell vials, 50 ants to a vial. The ants were then shaken into the P³² solution 100 or 200 at a time. As soon as the mass of ants had become thoroughly immersed and wetted in the solution the cup was raised and the excess solution drained back into the jar. Usually less than a minute was required for soaking. The sieve cup was then removed from the jar, inverted over a large paper towel or piece of filter paper and all of the wet ants shaken out onto the paper. A few taps with a glass rod on the bottom of the screen sufficed to dislodge all of the ants. As soon as the ants had dried out and were beginning to move about, the paper was placed next to the hill and the ants allowed to crawl back under the stone on their own accord. Any injured or abnormal appearing individuals were removed so that only active, uninjured ants were returned to the hill. Mortality during the tagging process was less than one %. For colonies which were obviously small (as indicated by a small mound or a small mass of ants in the galleries) about 400 ants were tagged; for large colonies as many as 1000 were tagged.

Ants were tagged from a total of 8 colonies ranging from small ones to what appeared to be the largest ones in the area. The first recapture sample was taken one or two days after tagging by lifting the stone and aspirating ants from the galleries. In the case of 6 colonies a 2nd recapture sample was taken 4 to 6 days after tagging. Ants in the recapture samples were killed (in a killing jar) and tested for radioactivity. To facilitate the test-

ing of large numbers of ants, use was made of a scanning machine in the Department of Agriculture at Oxford. The scanning system consisted of a belt of paper moving under a shielded detector (Geiger tube) which activated a pen recorder. The motors driving the belt and the record were electrically synchronized. The ants were laid out in rows on ruled paper and held in place by a long strip of cellophane tape. The strip of ants was then fastened to the belt so that individual ants moved slowly one by one past the detector, while the pen automatically recorded those which were radioactive. The number of peaks on the recording chart thus constituted the number of marked ants in the recapture samples. The use of scanning systems for this and other ecological purposes is described elsewhere (Odum, Martin and Loughman 1960).

The authors are indebted to Charles Elton, Director of the Bureau of Animal Population, for providing facilities for the field work and to Drs. B. C. Loughman and R. P. Martin who provided the P³² and the scanning apparatus.

RESULTS

Population density (w) for 8 different colonies and the variance for each estimate are shown in Table I. Density was calculated from marking-recapture data using the unbiased formula (see Bailey 1951, Leslie 1952) as follows:

$$N = \frac{T(n+1)}{t+1} \text{ where } N \text{ is total number in the}$$

colony, T the number tagged, n the number recaptured, and t the number of marked individuals in the recapture sample. Variance was calculated as follows:

$$V = N^2 \frac{n-t}{(n+1)(t+1)}$$

The estimates indicate that the smaller colonies had 2000-3000 workers while the large colonies had as many as 10,000. For colonies 1-6, two estimates were made on the basis of recapture samples 1-2 days after tagging, and again 4-7 days after tagging. Considering the wide variance inherent in marking-recapture experiments the agree-

TABLE I. July density of worker's and total queen production in 8 colonies of *Lasius flavus*

Colony	No. tagged	Sample 1	Recapts.	Sample 2	Recapts.	NUMBER OF WORKERS			1958 Alate queens Q
						w ₁	w ₂	w _t	
1	500 30.vii.	437 31.vii.	68	46 5.viii.	10	3174 ± 348	2136 ± 540	3063 ± 313	14
2	600 30.vii.	321 31.vii.	89	134 5.viii.	19	2147 ± 191	4050 ± 915	2150 ± 212	34
3	500 6.viii.	189 8.viii.	17	153 10.viii.	11	5278 ± 1152	6417 ± 1709	5914 ± 1033	240
4	500 6.viii.	186 8.viii.	8	150 10.viii.	10	10389 ± 3205	6864 ± 1908	8868 ± 1923	192
5	500 6.viii.	149 8.viii.	7	159 10.viii.	11	9375 ± 3041	6667 ± 1778	8131 ± 1759	153
6	500 6.viii.	97 8.viii.	7	157 10.viii.	19	6125 ± 1956	3950 ± 806	4722 ± 844	55
7	1000 16.viii.	243 18.viii.	21	—	—	11091 ± 2206	—	11091 ± 2206	306
8	400 16.viii.	98 18.viii.	17	—	—	2200 ± 456	—	2200 ± 456	4

ment between the 2 estimates was reasonable but not as good as had been hoped.

The number of queens (Q) produced by each of the colonies is also shown in Table 1, and is plotted against density (W) in Figure 1. It is evident from Fig. 1 that there was a fairly good relationship between the number of workers and queen production. Regression analyses showed that a better fit to a straight line was obtained with Q against W_2 than against W_1 . In other words, queen production seemed better correlated with density based on recaptures 4-7 days as compared with 1-2 days after sampling. Subsequent work with another species of ant has indicated that 24-48 hours is often not long enough to allow proper mixing of the tagged and untagged ants (Golley, Odum and Gentry 1960). In using P^{32} for tagging ants we would recommend that recapture samples be taken about a week (5-10 days) after tagging. Because of the short half-life of P^{32} and the rapid biological turnover, the probability of losing a recognizable "tag" would increase after 10 days. For maximum accuracy with individual colonies a continuous marking-recapture procedure employing a radionuclide with a longer half life and slower turnover would be desirable. However, for estimating density over a large area involving many colonies the procedure used in this study seems quite satisfactory. A procedure involving a single tagging using an isotope with a short half-life followed by the taking of a single recapture sample has many advantages for ecological work since disturbance of the colonies and the amount of radioactive solution needed are both kept to a minimum. Experiments could be repeated at monthly intervals without detectable contamination of the soil or other part of the environment.

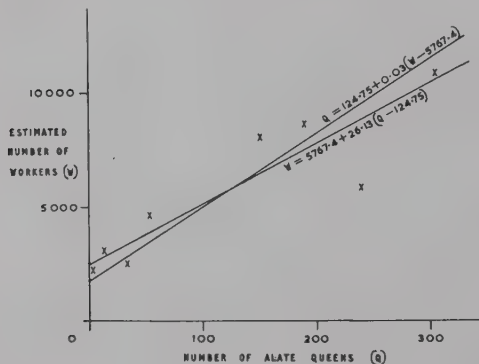


FIG. 1. The number of queens (Q) produced annually plotted against estimated number of workers (the W_t values in Table 1) as determined by marking-recapture experiments in 8 colonies of *Lasius flavus*. Regression lines calculated for W_t on Q and Q on W_t are shown. The deviation from the origin has a P of about 0.05 of being due to chance alone ($t = 2.57$).

Since the number of queens produced during the summer was in rough proportion to the number of workers in the tagged colonies, and since queen production for all colonies in a prescribed study area was known, the regression equation (see Fig. 1) was used to calculate density of workers in all of the untagged colonies of the study area. Colonies of a related species, *Lasius niger*, were present in a portion of the area occupied by colonies of *L. flavus*. *L. niger* tends not only root aphids, as does *L. flavus*, but also aphids living on the above-ground

portion of the grasses and forbs. In a 23 square meter portion of the study area containing some of the tagged colonies of *L. flavus* but no colonies of *L. niger* the average worker density of the former was 1130/M². Since the average live weight of an individual worker is about 1.2 milligrams, the average living biomass was 1.36 grams/M². In a 162 M² portion of the grassland containing scattered colonies of *L. niger* the density of *L. flavus* was computed to be 420 workers/M² or 0.5 gms/M². Density for the entire 277 m² study area in which the number of queens was measured averaged 485 workers/m² or about 0.6 gms/M².

Pontin (1958) had previously demonstrated by experimental manipulation of colonies in the field that the 2 species of *Lasius* are in partial competition, but coexist in the same area in a stable equilibrium. When a colony of one species was destroyed by poison, queen production in adjacent colonies of the other species increased the following year.

Pickles (1940) has made estimates of density of *L. flavus* and other species of ants by laboriously digging out a Yorkshire hillside study area of 880 M² annually for 5 years in succession. Colonies of *Lasius* contained from a few hundred up to about 6000 ants but the over-all density was only 13/M² for *Lasius* and 17/M² for all ants during the first year; density declined in subsequent years probably because of the disturbance of digging out the colonies. *Lasius flavus* also occurs in North America, but we have seen no density estimates of such populations. The habits of the species in America may be different since Wilson (1955) reports that surface mounds are not constructed.

Determining density, of course, is but the first step in understanding the impact of the population on the grassland community. Presumably, 400-1100 ants/M² through the medium of their aphid colonies consume an appreciable fraction of the net primary production, but the magnitude of this consumption cannot be estimated until metabolic rates and production rates of the ants and aphids are better known. The root-aphid-*Lasius* food chain would seem an ideal one for the study of energy flow.

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THE SPAWNING OF *NEANTHES SUCCINEA* IN THE SALTON SEA¹LARS H. CARPELAN² AND RICHARD H. LINSLEY*Department of Zoology
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The spawning of the polychaetous annelid *Nereis limbata* was observed in the Woods Hole region by Lillie and Just (1913) who reported considerable uniformity in spawning periods in accordance with phases of the moon. Lillie and Just concluded that periodicity in *Nereis limbata* belongs to the large class of phenomena of which lunar spawning of the Pacific palolo, *Eunice viridis*, is a well-known example. Korringa (1947) in a review of the relations between the moon and periodicity in the breeding of marine animals pointed out that *Nereis limbata* was not a clear cut case of lunar periodicity. The synonymy of this species is extensive (see Hartman 1951). What Lillie and Just referred to as *Nereis limbata* is probably the same species currently known as *Neanthes succinea* (Frey and Levicart).

Since the time when *Neanthes* was first reported present in the Salton Sea by Hartman (1936), it has become very prevalent and is the main food of the croaker, *Bairdiella chrysotis*, a fish introduced into the Salton Sea from the Gulf of California in 1951. The life cycle of *Neanthes* was studied during 1955-1956 as part of a study of the Sea as a sport fishery. The ichthyological aspects of the study are to be published as a Fish Bulletin by the California Department of Fish and Game. Because the phenomenon of periodicity may be of general interest, the following note is submitted for wider dissemination of evidence that, at least in the Salton Sea, the spawning of *Neanthes* does not seem to follow a monthly cycle.

Observations in the field and in the laboratory indicate that spawning takes place as described by Lillie and Just. Spawning can be observed at night because mature *Neanthes* are attracted to light. Epitokes appear shortly after sunset, swimming at the surface; maximum numbers are seen about an hour after sunset; numbers then decrease until, about 3 hours after sunset, epitokes are no longer attracted to the light and their spawning, apparently, ceases for the night. Fertilization takes place immediately after eggs are spawned. At temperatures between 20-25° C, the eggs begin to cleave within 20 minutes after fertilization, develop into ciliated, free-swimming larvae in about 13 hours, and into trochophore larvae within 24 hours after fertilization. Thus, the presence of eggs in the plankton would seem to be presumptive evidence for spawning within the previous 24 hours. Eggs were found by the senior author in quantitative plankton samples taken at all phases of the moon. For example, eggs were present in all samples collected during a 4-month period on the dates and at the phases of the moon indicated in the following list:

It was mentioned above that within 24 hours after fertilization development has proceeded to the trochophore stage. A day and a half after fertilization, the larva has developed 2 segments with setae, and after 2 days there are 3 seta-bearing segments. The larvae remain planktonic and continue to add segments until, after about 2 weeks, they have attained 6-9 segments and settle to begin

TABLE 1. Dates of Plankton Collections, Salton Sea November 1955 to March 1956

Date of Sample	Date of Moon Phase
November 2, 1955.....	Full, October 31
November 15.....	New, November 14
November 28.....	Full, November 29
December 13.....	New, December 14
January 4, 1956.....	Last Quarter, January 4
January 16.....	New, January 12
February 3.....	Last Quarter, February 3
February 14.....	New, February 11
February 29.....	Full, February 25
March 19.....	First Quarter, March 19

their bottom-dwelling period. The junior author studied the recently-settled worms by suspending one-gallon jars beneath the surface at various locations throughout the Sea. Jars removed and replaced at 10-day intervals indicated irregular periods of maximum spawning each month. The time of occurrence of a monthly peak of spawning could differ at 2 locations relatively near each other. For example, whereas 90% of the worms settling during the month of March 1955 at a station 100 yards offshore from the laboratory at Fish Springs settled during the last 10 days of the month, at a station 2 miles to the south of Fish Springs only 22% of the total number that settled there during the month of March settled in the same 10-day period (the last 10 days of the month). At this second station the period of maximum settling was the first 10 days of March, during which period 70% of the monthly total settled. The size of worms in the 2 samples was the same; assuming that there were no differences in the length of the planktonic period of the worms spawned in the 2 locations, the period of maximum spawning could not have occurred at the same phase of the moon. That is, although data from one station indicated greater activity at one phase of the moon, data from a nearby station showed greater activity at another phase.

Furthermore, although there might be, as in the preceding example, one period of maximum spawning during a month, there might be more than one period, or the spawning could be diffused throughout the month. For example, at the station 100 yards offshore from Fish Springs 10% of the total number of worms that settled during May 1955 settled during the first 10 days, 45% settled during the second 10 days of the month, and 45% settled during the last 10 days. The 10-day settling jars thus showed no regularity in peaks of spawning (as indicated by settling) each month, nor any correlation with phases of the moon.

Although no monthly period of spawning was found, there was evidence of annual periodicity of spawning in the Salton Sea. *Neanthes* spawns there the year around, as evidenced by eggs being present in the plankton during every month of the year. Evidence from 30-day settling jars verified the year-round breeding observed in plankton collections and, like the plankton samples, indicated annual peaks of breeding activity. In the 30-day settling jars, of the total number of worms that settled during the

¹ Supported by an agreement, WCB-108, between the University of California and the State of California Department of Fish & Game, under the direction of Dr. Boyd W. Walker, Department of Zoology, University of California, Los Angeles.

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year, 65% settled from March through June, 8% from July through October, and 27% from November through February. There is thus an annual peak of spawning in spring, a secondary maximum during fall and winter, and relatively little spawning during summer.

The Salton Sea has a salinity near that of the ocean and has a marine-like fauna, but it is hardly a typical marine habitat. (The environmental aspects of the Sea have been discussed by Carpelan 1958). It may be, therefore, that the spawning of *Neanthes* in the Salton Sea follows a different pattern than it does in the ocean, and represents a special case from which no generalization regarding the spawning habit of this worm can be drawn. However, the data presented may be evidence in support of the view of Korrington that the spawning habit of *Neanthes* is not a case of lunar periodicity.

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ON THE DISTRIBUTION OF FOREST SOIL MICROARTHROPODS AND THEIR FIT TO "CONTAGIOUS" DISTRIBUTION FUNCTIONS

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INTRODUCTION

Surveys of soil metazoa showed that Collembola and Acarina constitute 75 to 80% of the total number of arthropods (Thompson 1924, Edwards 1929, Ford 1935, 1938, Baweja 1939, Salt *et al.* 1948, Macfayden 1952). Evans (1955) estimated 2.5 mites per cc of soil in a spruce plantation. In the same volume of soil Wallwork (1957) estimated 2.35 mites in a hemlock forest. Most of these organisms are beneficial in promoting soil fertility through their roles as fungivores and in accelerating decay of wood (Hartenstein, in preparation). In view of their density, these organisms are very important to soil formation.

Recent studies of some effects of chemical treatment on soil microarthropods have indicated the need for knowing their spatial pattern of distribution (Hartenstein 1959, Stegeman in preparation). An analysis of the data of plot microarthropod-counts (Hartenstein 1959) on 4 pretreatment occasions revealed a nonnormal distribution. These distributions were based on a sample size $n = 24$; each sample consisted of 12 cores (1" diameter by 3" depth) of soil. It was not known whether the spatial distributions of the organisms in single cores or in the composite 12 core sample were random (Poisson) or contagious. The distributions were skewed to the right and were characterized by variances which greatly exceeded their means. A square root transformation resulted in data amenable to an analysis of variance as discussed in that report. However, in theory, a square root transformation is strictly applicable to data distributed in Poisson form (Beall 1954, Fisher 1954). Therefore, a knowledge of the mathematical model to which the observed distribution density could be fitted might have allowed a more accurate transformation.

This paper is concerned with the spatial distribution of free-living forest soil mites and Collembola termed, collectively, microarthropods.

The forest floor can be thought of as a continuum of space which can be divided into many arbitrarily small units. If a unit is chosen such that, relative to the entire area being sampled, the probability p of obtaining micro-

arthropods is rather low relative to the probability q of not obtaining these organisms, and if the distribution of microarthropods is uniform over the entire area sampled, implying that each individual is distributed independently of other individuals, this distribution can usually be characterized or defined by the Poisson. A derivation and discussion of the Poisson is given in Fraser (1958). A chi-square test, $\chi^2 = \sum (E - O)^2 / E$ may be employed to determine whether the departure of the observed values, O , from the expected Poisson values, E , is significant. If the departure is not significant, the observed distribution is assumed to be consistent with this model.

The spatial distribution of animals is rarely random and therefore in conformity with the Poisson. Rather, for various purposes including reproduction and attraction to food, animals aggregate so the probability of infestation is not equal for all sampling units. The probability density function of occurrence of animals in a single unit increases or decreases directly with the number of organisms and results in a contagious distribution for which several mathematical models have been derived. These include the Thomas (1949), Neyman's A, B, and C (1939), the Polya-Aeppli (1930), the negative binomial (Fisher 1941), the discrete lognormal (Preston 1948) and the Cole (1946). Using factorial cumulants, Anscombe (1950) arranged these distributions, excluding that of Cole, in order of increasing skewness and tail length as presented above. He also showed how the shapes of the curves change with substantial changes in the values of a parameter, p . Each of the above distributions is a generalized form of the Poisson. They are based upon the notion of a distribution of colonies with a mean m_1 within which are distributed individuals having a mean m_2 . The colony distribution is assumed Poisson and the individual distribution may be Poisson (Thomas, Neyman), logarithmic (negative binomial), geometric (Polya-Aeppli), or arbitrary (Cole).

The properties common to each of these distributions are a positive skew and a variance that exceeds the mean. The skew is characteristic of animal or plant distribution regardless of the value p since it is impossible to obtain

quadrats or cores or other land areas with negative values of organism density. The excess variance is attributable to aggregation.

If it is known that a specific or other taxonomic group of organisms is spatially distributed such that its observed density values will fit a binomial, Poisson, or negative binomial distribution, this knowledge can be useful in at least three ways: (1) to compare the estimated means of populations in different localities or within the same locality but exposed to various treatments, (2) to estimate the population mean and its experimental error over consecutive periods in growth studies, including studies of predator and prey relations and (3) to develop a sequential sampling plan for surveys (Waters 1955). The negative binomial distribution is the only contagious distribution useful in the above ways since it is the only one for which sampling theory (Bliss and Fisher 1953) has been developed. If it is known that an organism is distributed spatially in conformity with the Poisson or negative binomial model, the data obtained in (1) or (2) above may be transformed as shown by Beall (1954) and thus made amenable to analysis.

METHODS

Sampling was conducted in a mixed hardwood stand in the Tully Forest, New York. This stand was an uneven aged stand of sugar maple (*Acer saccharum* Narsh.), white ash (*Fraxinus americana* L.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula lutea* Michx.) and eastern hemlock (*Tsuga canadensis* (L.) Carr). The understory consisted of a number of grasses, ferns, and seasonal wild flowering perennials common to the northeast. The soil belonged to the Lordstown series (Cline 1957).

Two areas were sampled within the stand. In area I, 10 stakes were driven into the ground at 25 yard intervals. This area was sampled at 4-week intervals, beginning in July, to obtain collections 1, 2, and 3. The soil temperature ranged from 60 to 62° F for collections 1 and 2 and from 61 to 64° F for collection 3. The corresponding ranges of soil moisture were 41–57%, 31–52% and 34–48%. A single plot, 10 feet by 30 feet, was established in area II from which collections 4, 5, and 6 were obtained. These collections also were taken every 4th week beginning in July. The soil temperature and moisture ranges corresponded to those of collections 1-3. Samples were removed in the morning for each collection date.

Four sampling schemes were used. For collection I, 10 samples were removed from within a 12-inch radius of the stake. A similar number of samples was removed from a 5-foot radius for collection 2 and from a 15-foot radius for collection 3. Samples were taken at approximately 6-inch intervals in area II. The plot was divided into thirds and a single 10-foot square section was sampled on a collection date.

The samples consisted of cores of soil of 2 cm diameter and 7.5 cm in length. These cores were removed at random with a core sampling tool and transferred directly to a polyethylene bag. Groups of 20 bags were placed in separate boxes to prevent crushing and transported immediately to the laboratory. Each sample was placed in a quart-size Berlese funnel and extracted of organisms (Macfayden 1953).

Counting followed the procedure of Hartenstein (1959). Where possible, species were tallied. Tests were conducted to determine the fit of 6 groups of organisms to the expected distribution function. These included (1) *Steganacarus diaphanum* Jacot 1930, a species which feeds upon decayed wood, (2) morphologically similar appearing mites from the families Haplozetidae, Oribatul-

idae, and Ceratozetidae, referred to hereafter as the Haplozetid complex, (3) the suborder Oribatei which also included groups 1 and 2, (4) the order Collembola, members of which feed upon fungi and decaying plant material, (5) the genera *Veigiaia* and *Parasitus*, predatory mites upon Collembola and upon the members of group 2, and (6) the total microarthropod community.

The data were fitted to the Neyman A distribution using the recurrence equation of Beall (1940) and to the negative binomial as presented by Bliss and Fisher (1953). The former distribution, in addition to having less skew and a shorter tail than the latter, also can have a distribution curve which is differently shaped and can have more than one mode. Significance of fit was determined with a chi-square test.

RESULTS AND DISCUSSION

The observed and expected distribution data are presented in Table I together with the mean and variance for each group of organisms and the corresponding k statistic. The latter is a parameter value associated with the negative binomial function.

For economy in printing all expected Poisson values have been omitted. The fit of the Poisson to the observed was good only for *S. diaphanum* of collection 3, and the predacious mites in the same collection.

The variation between the expected negative binomial values and those observed is within experimental error in all but 3 cases. Excessive variation between the expected and observed values of Oribatei densities in collection 1 and the Collembola densities in collection 5 is due to heterogeneous data. An inefficient estimate of k is perhaps the cause of the poor fit to the distribution of predaceous mites in collection 6.

The observed values failed to fit the Neyman model for all groups or organisms in collection 1 except *S. diaphanum*. They also had failed to fit the total counts for collections 1, 2, 5, and 6, the Collembola count for collections 1, 4, and 5 and the Haplozetid mite complex count for collection 3. Discrepancies between the expected and observed values reflect the inadequacy of the model to define the spatial distribution. Lower probabilities for a greater chi-square in all but one instance reveals the superiority of the negative binomial over the Neyman in defining these distributions. Using chi-square as a basis for comparison, the negative binomial defined the distribution of the various taxonomic groups of organisms equally well.

The poor fit of both models to the Collembola distributions mentioned above might be explained by the behavior of these organisms. Many of the Collembola possess a furcula by which they are able to leap several inches. Consequently, when sampling with a core remover, the opportunity is present for escape. There also appears to be a greater tendency to leave the soil sample prior to extraction. These 2 factors may be operating against a "natural" distribution and thus reflecting inadequacies in sampling procedure.

Although the negative binomial distribution suitably defined the distribution of microarthropods, it cannot serve to explain the cause of the spatial arrangement. However, laboratory observations over a 9-month period have shown that this group of organisms manifests contagion in their natural distribution. When they are extracted from soil and kept within the 7 cm area of a filter paper, the oribatids aggregate about choice food sites. Often these sites "appeal" to the Collembola, resulting in increased aggregation. In consequence, predaceous *Veigiaia* and *Parasitus* are attracted to these sites indirectly. Although *S. diaphanum* is invulnerable to

TABLE I. Frequency distributions of microarthropods in a mixed hardwood stand. For each collection, the number of samples (f) harboring $n = 0, 1, 2 \dots$ microarthropods has been fitted by a Neyman A (Ney ϕ) and a negative binomial (NB ϕ) distribution. ($\bar{x}$ = mean, s^2 = variance, k = parameter used in computing negative binomial).

Collection 1

$\bar{x}=0.47$ $s^2=0.80$ <i>S. diaphanum</i> $k=0.6740$			<i>Veigilia</i> and <i>Parasitus</i> $\bar{x}=0.69$ $s^2=1.03$ $k=1.1688$			$\bar{x}=0.88$ $s^2=1.85$ Collembola $k=0.6626$			$\bar{x}=1.84$ $s^2=6.03$ Oribatei $k=0.7732$			$\bar{x}=3.44$ $s^2=10.30$ Total $k=1.0267$			
n	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ
0	141	140.0	141.4	116	116.0	116.6	114	113.7	117.0	78	78.0	96.9	42	44.2	45.4
1	38	38.7	34.8	52	50.5	49.0	41	43.2	34.3	46	42.4	18.2	32	34.9	20.9
2	12	13.3	15.5	18	20.4	22.1	20	20.6	24.0	16	26.4	22.5	26	27.3	25.8
3	5	4.8	5.5	8	8.0	8.3	15	10.5	13.0	24	17.2	19.8	26	21.2	22.6
4	3	1.8	1.8	5	3.1	3.3	4	5.5	6.3	15	11.4	14.6	23	16.4	17.1
5	1	1.4	1.0	1	2.0	0.9	3	3.0	2.9	4	7.6	9.9	16	12.7	16.0
6+							3	2.5	1.9	6	5.2	6.5	12	10.0	12.0
7										4	3.5	4.3	4	7.7	9.0
8+										7	8.3	8.3	2	6.0	7.1
9													3	4.6	4.6
10+													14	15.0	19.5
P (X^2)		0.60	0.06		0.76	0.52		0.61	0.30		0.04	<.001		0.10	0.05

Collection 2

$\bar{x}=0.26$ $s^2=0.42$ <i>S. diaphanum</i> $k=0.3595$				Haplo- zetid $\bar{x}=0.96$ $s^2=1.68$ Complex $k=0.1326$			Ori- batei $\bar{x}=1.11$ $s^2=5.15$ $k=0.6685$			<i>Veigilia</i> and <i>Parasitus</i> $\bar{x}=0.43$ $s^2=0.91$ $k=0.92$			Collembola $\bar{x}=1.26$ $s^2=4.12$ $k=0.4700$			Total $\bar{x}=2.58$ $s^2=7.02$ $k=1.5049$		
n	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ
0	164	164.0	163.9	164	164.0	170.2	104	104.0	148.7	140	140.0	153.6	103	102.7	122.9	45	44.5	58.4
1	24	25.0	23.7	14	16.8	5.4	51	43.4	4.3	44	41.3	22.1	36	36.6	14.7	41	42.2	26.9
2	8	7.2	8.8	9	7.4	7.3	21	22.6	7.9	13	12.7	13.8	28	20.4	18.2	33	33.4	29.4
3	3	2.4	2.5	4	4.0	6.6	10	12.5	9.7	1	3.9	6.3	13	12.8	15.7	25	24.6	24.9
4	1	1.8	1.1	5	2.5	4.6	5	7.2	9.1	1	1.2	2.5	6	8.3	11.0	22	17.5	19.0
5+				4	3.7	5.9	9	10.3	20.3	1	0.9	1.7	3	5.6	6.9	13	12.5	11.3
6													2	3.9	4.2	6	8.7	9.4
7													2	2.7	2.5	1	5.9	6.2
8+													4	5.1	3.9	4	4.0	4.0
9																3	2.7	2.5
10+																7	4.0	8.0
P (X^2)		0.71	0.74		0.35	<.001		0.43	<.001		0.20	<.001		0.20	<.001		0.31	<.02

Collection 3

$\bar{x}=0.20$ $s^2=0.20$ <i>S. diaphanum</i> $k=10.0000$			Haplozetid Complex $\bar{x}=0.32$ $s^2=0.59$ $k=0.2980$			$\bar{x}=0.62$ $s^2=0.11$ Collembola $k=0.7137$			$\bar{x}=0.93$ $s^2=1.81$ Oribatei $k=0.9806$			$\bar{x}=1.43$ $s^2=3.79$ Total $k=1.6760$		
n	f	NB ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ
0	164	164.0	160	160.5	174.4	128	127.7	129.6	104	104.0	109.7	61	61.0	74.6
1	32	32.1	25	24.9	15.1	42	42.5	37.0	49	49.6	39.4	54	51.9	39.1
2	4	3.9	8	8.4	7.0	16	17.0	19.7	26	23.9	25.8	36	35.2	33.5
3			4	3.3	2.3	7	7.1	8.4	11	11.5	13.5	19	21.5	21.6
4			3	2.9	1.2	6	3.1	3.2	4	5.6	6.4	14	12.8	12.1
5+						1	2.6	2.1	6	5.4	5.2	5	7.3	6.7
6												4	4.1	3.5
7+												7	6.2	8.9
P (X^2)				0.91	<.01		0.29	0.20		0.94	0.22		0.96	0.08

Collection 4

n	$\bar{x}=0.50$ $s^2=0.07$ <i>S. diaphanum</i> k=1.5592			Haplozetid Complex $\bar{x}=1.10$ $s^2=1.67$ k=2.7561			Oribatei $\bar{x}=2.37$ $s^2=5.80$ k=1.3860			$\bar{x}=2.24$ $s^2=5.12$ Collembolus k=1.7913			Total $\bar{x}=4.66$ $s^2=11.14$ k=2.4100		
	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ
0	130	130.1	133.5	82	79.3	65.6	49	50.0	56.9	42	46.9	57.3	16	15.0	16.0
1	51	48.9	44.8	59	62.3	55.8	45	43.8	31.8	61	46.6	35.0	21	23.7	18.7
2	12	15.0	15.7	34	33.4	38.2	37	33.0	31.9	28	36.0	33.3	26	26.7	23.9
3	5	4.3	3.9	12	15.1	21.5	19	23.4	25.6	26	25.2	25.8	29	25.9	25.4
4	1	1.2	0.7	9	6.2	10.7	14	16.2	18.6	10	16.8	18.2	20	23.0	24.3
5+	1	0.4	1.0	4	3.3	6.8	12	11.0	12.9	13	11.1	12.1	17	19.5	21.5
6							11	7.4	8.1	7	7.1	7.7	15	15.8	17.9
7							5	4.9	6.0	5	4.5	4.7	15	12.6	14.2
8+							8	10.3	8.2	6	2.8	2.8	9	9.7	10.7
9										2	3.0	3.0	12	7.4	7.9
10													7	5.5	5.5
11													3	4.1	3.8
12+													10	8.0	10.2
P (X ²)		0.31	0.17		0.48	0.05		0.51	0.06		<.01	<.001		0.78	0.72

Collection 5

n	$\bar{x}=0.24$ $s^2=0.35$ <i>S. diaphanum</i> k=0.5410			Haplozetid Complex $\bar{x}=0.76$ $s^2=1.30$ k=2.0270			Collembola $\bar{x}=0.75$ $s^2=1.36$ k=0.6332			Oribatei $\bar{x}=1.44$ $s^2=2.80$ k=1.4080			Total $\bar{x}=2.34$ $s^2=4.79$ k=1.5890		
	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ	f	NB ϕ	Ney ϕ
0	164	164.0	165.0	94	94.0	95.0	122	122.0	120.0	74	74.0	78.4	45	47.3	46.6
1	28	27.2	24.8	62	59.3	56.6	40	41.8	39.4	55	52.8	44.2	48	44.9	38.5
2	5	6.4	7.6	22	27.8	29.0	14	18.5	22.7	27	32.2	33.1	31	34.6	36.0
3	2	1.7	1.8	13	11.5	12.3	16	8.9	10.5	22	18.5	19.6	31	24.7	29.6
4	1	0.7	0.8	7	4.5	4.5	6	4.3	1.9	7	10.3	11.4	15	16.8	13.1
5				2	2.9	2.6	2	4.5	5.4	8	5.6	6.0	10	11.2	12.1
6+										7	6.6	7.3	9	7.4	7.0
7													4	4.7	2.8
8+													7	8.4	14.3
X ²		0.48	0.25		0.50	0.26		.02	.03		0.31	0.12		0.76	<.02

Collection 6

n	$\bar{x}=1.96$ $s^2=2.87$ k=2.14			<i>Veigiata</i> and <i>Parasitus</i> $\bar{x}=0.25$ $s^2=0.36$ k=0.1285			Collembola $\bar{x}=1.42$ $s^2=4.28$ k=0.5396			Total $\bar{x}=4.30$ $s^2=15.03$ k=1.4428			Haplozetid Complex $\bar{x}=1.51$ $s^2=2.60$ k=1.6700		
	f	NB ϕ		f	NB ϕ		f	NB ϕ		f	NB ϕ		f	NB ϕ	
0	50	49.7		164	163.0		100	99.7		35	34.8		68	68.0	
1	49	50.8		26	16.6		32	38.7		40	35.2		49	53.9	
2	35	38.1		6	14.1		20	21.7		17	30.2		38	34.2	
3	28	25.1		4	6.3		18	13.3		29	24.3		24	19.8	
4	16	15.4					9	8.5		11	19.0		10	11.0	
5	13	8.8					8	5.6		16	14.5		6	5.9	
6+	6	5.0					4	3.7		12	10.9		5	7.2	
7+	3	7.1					5	2.5		12	8.1				
8							3	1.7		4	6.0				
9							1	4.4		8	4.4				
10										5	3.2				
11+										11	9.4				
P (X ²)		0.10			<.001			0.55			0.04			0.31	

predation by *Veigiaia* and *Parasitus*, its mode of reproduction leads to aggregation. Eggs are deposited upon decaying wood by the rather sessile female. The larva feeds upon the wood, remaining in the vicinity of its birthplace throughout its life and giving rise to progeny and a repetition of the cycle. Thus, the whole community is closely related and contagious distribution is evidenced.

SUMMARY

A study was conducted to determine the fit of observed distributions of forest soil microarthropods to the expected Poisson, negative-binomial, and Neyman-A distribution functions. Four sampling plans were tested on 6 occasions in 2 areas of a mixed hardwood forest. The distributions of 6 groups of organisms were fitted to the above distribution functions. These groups included (1) *Stegancarus diaphanum*, (2) the morphologically similar families Haplozetidae, Ceratozetidae, and Oribatulidae, (3) the suborder Oribatei including the organisms previously mentioned, (4) the predaceous mites of the genera *Veigiaia* and *Parasitus*, (5) the order Collembola, and (6) the total community of microarthropods. The observed distributions fitted the Poisson distribution function in only 1 of 31 cases and thus the distributions were not random. Conversely, the negative binomial fitted well in all but 3 of 31 tests. The Neyman-A density function fitted well in 13 of 25 tests but in only 1 instance fitted the observed distribution data more closely than the negative binomial. Chi-square probabilities indicated equally good fitting of the negative binomial to the 6 groups of organisms. Ecological evidence was presented to indicate contagion in the distribution of the community in nature.

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OBSERVATIONS ON THE FEEDING BEHAVIOR OF WHITE-TIP SHARKS ON SCHOOLING FISHES

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The white-tip, *Pterolamiops longimanus*, is the surface shark most frequently encountered beyond the continental shelf in the Gulf of Mexico and Caribbean Sea. Numerous captures have been made from the exploratory vessel *Oregon*, particularly while tuna longline fishing, and many of the early observations were among those

recorded by Backus, Springer and Arnold (1956). Of particular interest in later observations from the *Oregon* however, was the presence of small tunas (weighing approximately 5 to 15 lb) in the stomachs of some of the captured white-tips. The fish, 1 to 3 in each of the stomachs containing tuna, were in various stages of diges-

tion, but a few could be identified as *Katsuwonus pelamis* and *Thunnus atlanticus*. There were no indications that these fish had been taken from hooks or had suffered any crippling injuries which would have enabled the sharks to "run them down." Backus, *et al.* found similar stomach contents in white-tips from other captures.

An explanation of at least one method of capture of such active swimmers was apparent after observations from the *Oregon* on Cruise 62, north of the Virgin Islands in September 1959. Late one afternoon, about 2 miles off the 100 fathom curve, a strong tide-rip paralleled the shelf contour for several miles, and along the rip were continuous schools of tuna feeding on numerous but scattered small Spanish sardines, *Sardinella anchovia*. Several passes through the schools with trolling lines resulted in the capture of 9 blackfin tuna, ranging from 3 to 16 pounds. The tuna schools were very dense and the feeding behavior of the tuna was typical—fast darting rushes at the surface with frequent leaps clear of the water. It is difficult to describe the frenzied cut and slash of small schooling tuna working bait fish.

Mixed with the tuna were many white-tip sharks, ranging from about 3 to 6 feet in length. Each shark was swimming slowly in a rather erratic, sinuous course with its snout protruding from the water, its mouth wide open at just about the surface level. At one point, the sharks were so numerous that they were spaced not over 10 feet apart in an area some 50 feet wide by 300 feet long. No attempt was made by the sharks to chase after or snap at the hundreds of tuna in the same area. It was an inescapable conclusion, however, that the white-tips were merely waiting and ready for those moments when tunas would accidentally swim or leap right into their mouths. The identical behavior of so many sharks, observed over a 30 minute interval, would indicate this to be a well-established feeding pattern. Only with the first hand observations, at close quarters, can one give complete credence to the likelihood that oceanic sharks obtain a segment of their food in the manner described.

There might seem to be the possibility that the white-tips were trying to scoop up the small *Sardinella*; how-

ever, the low schooling density of this species at the time appeared to make this quite profitless.

One somewhat similar example was cited by Springer (1957), where small blackfins were seen to leap into the mouth of a whale shark, which was "pumping" smaller fishes.

Another feeding observation was made in August, 1957, on *Oregon* Cruise 46 in the western Caribbean, at a position along the 500 fathom curve due north of Cape Gracias a Dios, Honduras. Sea conditions were rough with precipitous waves, but the wind had died off and the water visibility was quite good. Late in the afternoon a flock of about 20 red-footed boobies and white-bellied boobies were observed diving. We approached the area and saw that they were working on a tight, dense ball of small threadfins, *Polydactylus* sp. The ball was about 6 feet in diameter and, when first sighted, was within a foot of the surface. A few of the boobies were sitting on the water and reaching down to take big gulps of the threadfins. Lying alongside the school was a large white-tip (estimated 7 to 8 feet in length), which was biting off mouthfuls of fish, much in the manner of a person eating an apple. Apparently the school of threadfins was completely indifferent to the predation in progress and displayed no evasive action whatever. We attempted to drift the *Oregon* up to the school to dip-net a sample, but the violent roll of the vessel and the turbulence caused by the bilge keels apparently caused the school to sink down beyond the reach of the dip net. By this time the boobies had left, but we watched the white-tip continue to gnaw away at the school for several more minutes.

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SOME TEMPERATURE STUDIES ON THE BEETLE, *POPILIUS DISJUNCTUS*

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INTRODUCTION

These studies were initiated to investigate effects of prior temperature history upon the preferred temperature range of adult *Popilius disjunctus* (= *Passulus cornutus*). The relationship between upper lethal temperature and duration of exposure was also examined. These data for *P. disjunctus* ("Betsy beetles") are of particular interest, since the species is the only temperature zone representative of an otherwise tropical group. Adults dwell in rough tunnels in damp, rotting logs and stumps of deciduous trees, a habitat characterized by temperature and moisture stability. Since logs are not attacked until they reach a relatively advanced state of decay, the insect is not regarded as being of economic importance. The insect is an excellent experimental animal, being hardy, readily obtained, and easily handled (32-36 mm in length), and can be maintained with a minimum of difficulty in containers of moist, rotting wood.

DETERMINATION OF PREFERRED TEMPERATURE RANGE

The temperature gradient employed was similar to that of Fulton (1928), consisting of a galvanized metal trough (47 inches long, 6 inches wide, 3 inches deep). At one end, the trough extended 6 inches into a galvanized metal box (12" × 10" × 10") which served as a container for salt-ice mixture. The box was insulated with half-inch fiber board and equipped with a drain spout for water removal. The large trough contained a glass tube, 3 inches in diameter and 42 inches long, embedded in moist sand with only the upper curvature exposed. A 5-inch space between the end of the glass tube and the hot end of the trough facilitated introduction of test insects into the tube or test chamber. The smooth, curved sides of the chamber served to discourage climbing and aggregation. The test chamber was marked off into 6-inch sections numbered from 1-7 from the cold to the hot end. Each of these major subdivisions was in turn marked

off into 6 one-inch subdivisions. A 150 watt bulb was located immediately beneath section 7 (the hot end), a 75 watt bulb beneath section 6, and a 40 watt bulb beneath section 5. Since *P. disjunctus* exhibited a negative light reaction, the exposed dorsal portion and both ends of the glass tube were covered with removable metal covers, excluding all light from the test chamber.

After adjustment, a gradient of 1°C increment per inch was obtained, except for a greater magnitude of change toward either end. Extreme temperatures near the ends of the test chamber proved to be outside the normal activity range, and those below 9°C and above 33°C were generally avoided. Since the test insects were introduced into the hot end of the test chamber, it was frequently necessary to push them beyond the zone of high temperature to prevent injury that might occur before they could become properly oriented. Occasionally, an individual tipped onto its back in the cold zone and had to be righted and pushed into the more temperate range. These immobilized individuals were not included in tabulating data. Temperatures were read from a battery of 5 thermometers embedded in the sand along the tube. Another thermometer, placed in the test chamber, served as a reference point for detecting possible variation in internal and external temperatures. A Schultheis rapid recording thermometer ($0\text{--}50^{\circ}\text{C}$) was used to take readings between the permanently located thermometers. Water was added to the sand as needed to replace evaporation loss and to insure maximum heat conduction.

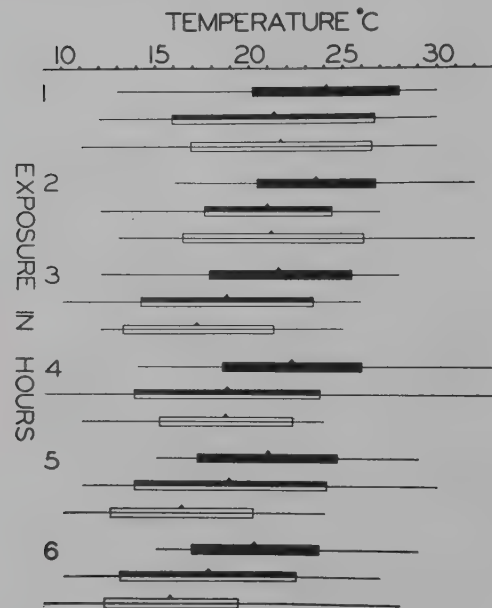


FIG. 1. Temperatures selected by adult *Popilius disjunctus* during 6 hours exposure in a temperature gradient. The point on the bar represents the sample mean ($\bar{y}$); the bar itself represents one standard deviation on either side of the mean ($\bar{y} \pm s$); the line through the bar indicates the activity range. Black bars: Test No. 1 (insects kept at $14\text{--}28^{\circ}\text{C}$); Black and open bars: Test No. 2 (insects acclimated at $13\text{--}15^{\circ}\text{C}$); Open bars: Test No. 3 (insects acclimated at $3\text{--}5^{\circ}\text{C}$).

When the device attained equilibrium, 10 beetles were introduced into the test chamber and left undisturbed for a 6-hour test except to record positions of the insects at half-hour intervals. Thus, with the position of each insect recorded at half-hour intervals, a total of 120 observations per replication was possible. Acclimation was accomplished by keeping beetles for several weeks in special thermostatically controlled temperature cabinets in which variation did not exceed $\pm 1^{\circ}\text{C}$. Insects were acclimated at 3 temperatures as follows: $14\text{--}28^{\circ}\text{C}$ (room temperature), $13\text{--}15^{\circ}\text{C}$, and $3\text{--}5^{\circ}\text{C}$. Figure 1 and Table I summarize the results of all preferred temperature range tests.

TABLE I. Summary of temperature selection data. Statistical symbols are those of Li (1957), $\bar{y}$ being the sample mean, s the standard deviation

	Test No. 1	Test No. 2	Test No. 3
Acclimation temperature ($^{\circ}\text{C}$).....	14-28	13-15	3-5
Length of acclimation.....	4 weeks	2 weeks	3 weeks
Number of insects.....	50	30	30
$\bar{y}$ (after 1 hour).....	24.1	21.3	21.7
$\bar{y}$ (after 6 hours).....	20.3	17.8	15.7
$\bar{y} \pm s$ (after 1 hour).....	20.2-28.0	15.9-26.8	16.9-26.6
$\bar{y} \pm s$ (after 6 hours).....	16.9-23.7	13.0-22.5	12.1-19.4
Activity range (after 1 hour).....	13-30	12-30	11-30
Activity range (after 6 hours).....	15-29	10-27	9-28

In order to learn whether the behavior of test insects was actually in response to the heat gradient rather than some tendency to remain near the center of the test chamber, 10 beetles were tested as previously described, but without ice or heat being added so that the temperature remained uniform throughout the length of the gradient. The results revealed random movements over the entire length of the test chamber, with a tendency for the insects to aggregate near the ends.

DETERMINATION OF UPPER LETHAL TEMPERATURE

Upper lethal temperature experiments were run in an electrically heated, thermostatically controlled temperature cabinet in which variation did not exceed $\pm 1^{\circ}\text{C}$ for a particular setting. For each temperature tested, 10 insects were placed in a battery jar and kept in the cabinet for one hour. The upper lethal temperature was taken to be that at which 80-100% of the test insects were killed. All insects were kept at room temperature ($14\text{--}28^{\circ}\text{C}$) for at least one month prior to being tested. Low humidity prevailed in these tests, although it doubtlessly varied somewhat. No attempt was made to determine the effect of different humidity levels on the upper lethal temperature.

In the first series of tests, 10 beetles were exposed to a temperature of 40°C for one hour. The procedure was then repeated, using 10 new insects, at 41°C , and so forth, until a temperature was reached that killed 100% of the test insects. After exposure of each group, the insects were observed and placed in containers of rotting wood to be observed again after 24 and 48 hours. Beetles were considered dead when mouth parts, antennae and legs failed to respond to extensive probing. The results of these tests are shown in Table II.

Another series of experiments was performed in order to determine the upper lethal temperature for a 12-hour period of exposure. These were identical to the one hour exposure tests described above, except that testing was begun at 35°C and repeated with a new group of test in-

TABLE II. Effects of one-hour exposure to high temperature

Temperature °C	Condition at conclusion of one hour exposure	Condition 24 hours later
42.....	No visible effects.	No visible effects.
43.....	None able to crawl actively.	All alive and apparently unharmed.
44.....	2 move well; 5 move feebly; 3 barely able to move antennae, legs and mouthparts.	All alive after 24 hours (6 dead after 48 hours).
45.....	8 move antennae, legs and mouthparts in a feeble manner; 2 dead.	1 able to move antennae, legs and mouthparts in a feeble manner; 9 dead.

TABLE III. Effects of 12-hour exposure to high temperature

Temperature °C	Condition at conclusion of 12 hours exposure	Condition 24 hours later
36.....	No visible effects.	No visible effects.
37.....	7 show no visible effects; 3 show reduced movement.	1 shows no visible effects; 3 walk with difficulty; 5 move legs, antennae and mouthparts feebly; 1 dead.
38.....	2 able to crawl actively; 4 move only legs, antennae and mouthparts; 4 dead.	2 able to move fairly well; 1 moves only legs, antennae and mouthparts in a feeble manner; 7 dead.
39.....	3 move appendages in a feeble fashion; 1 able to move mouthparts feebly; 6 dead.	All dead.

sects for each 1° C increase in temperature. The following results (Table III) were obtained:

DISCUSSION

P. disjunctus will select a preferred temperature range if given a wide series of temperatures from which to choose. Insects kept at low temperatures selected a lower range than those kept at intermediate or high temperatures; those kept at higher temperatures preferred a higher range than those kept at intermediate or low temperatures. Whereas the preferred temperature range is usually defined as a zone selected by 50-80% of the tested

individuals, in the present study, the preferred range is expressed as $\bar{y} \pm s$, which includes approximately 68% of the autoselected temperature preferences. The value of 68% is one of convenience and has no special physiological significance.

The findings indicate that regardless of previous temperature history, the mean selected temperature shows a tendency to decrease progressively during the course of a 6-hour exposure period (Figure 1). Because of this tendency, any statement of mean selected temperature or preferred range should be accompanied by a statement of duration of exposure if it is to be useful in comparative analyses. This apparent change in the preferendum was interpreted as a possible response to lower humidities at the cold end of the test chamber. Gunn and Cosway (1938) explained a similar shift to lower temperatures, and hence to a higher humidity, as an effort to avoid desiccation, initiated by critical reduction in water content of the insect's body.

The effect of length of exposure upon the upper lethal temperature is well demonstrated in the experimental findings. Whereas a one hour exposure to $45 \pm 1^\circ \text{C}$ is lethal to nearly all test insects, only $38 \pm 1^\circ \text{C}$ is lethal to most for a 12-hour exposure. According to Mellanby (1938), the difference is due to the increased role of desiccation as a contributing lethal factor in longer exposures. Humidity was not controlled in these experiments although low humidities prevailed in the temperature cabinet used. The upper lethals for both 1 and 12 hours of exposure approximate similar values reported for other temperate zone Coleoptera, but fall considerably short of those reported for most weevils (Spector 1956).

SUMMARY

When Betsy beetles were placed in a temperature gradient, they selected a temperature range, the nature of which depended upon past temperature history. A progressive decrease in preferendum, apparently in response to effects of desiccation, points out the necessity for accompanying preferendum data with a statement of exposure length. The upper lethal temperature for one hour exposure was approximately 45°C ; that for 12 hours exposure was approximately 39°C . Temperature characteristics of *P. disjunctus* do not differ greatly from those reported for most other temperate zone beetles.

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MEADOW MOUSE GIRDLING—ANOTHER CAUSE OF DEATH OF RESEEDED BITTERBRUSH PLANTS

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During 1957 and 1958, a population irruption of the meadow mouse (*Microtus montanus*) occurred in north-eastern California and Oregon. The mice moved from their normal habitat into marginal areas, including the sagebrush-bitterbrush type.

This type, even in its undisturbed condition, is far from ideal habitat, because the understory of perennial grass is generally not very dense and the grass dries early in the season. Meadow mice normally inhabit areas occupied by dense grass and herbaceous vegetation where some parts of the plants remain green during most of the growing season. Areas reseeded to bitterbrush (*Purshia tridentata*) are even less suitable for meadow mice than natural bitterbrush stands because site preparation for reseeded greatly reduces the understory.

Nevertheless, in 1957 and 1958 meadow mice girdled bitterbrush plants in natural stands and one reseeded stand.

The reseeded area in which the damage was found is located near Hallelujah Junction, in Lassen County, California. A hot wildfire had gone through the area in the summer of 1954 and it was reseeded to bitterbrush in the fall of 1954 and the spring of 1955. Initial stocking on the area was variable, ranging from about 150 to a little less than 1,100 seedlings per acre. These plants were subjected to extremely heavy use by jackrabbits and cattle, and many of them succumbed.

To find out what the growth of the bitterbrush plants

on this site would be if they were not grazed, a livestock-rabbit enclosure had been built to protect about 500 plants. These protected plants put on good growth and very few died until 1957 when meadow mouse girdling started (Figure 1). About 5% of the plants were completely killed by girdling and another 15% were damaged. About one-third of the partially killed plants were girdled in 1959 and the rest in 1957 and 1958.

In the fall of 1954 and the spring of 1955 the area had been trapped, and no meadow mice were caught during 300 trap nights. The major population buildup appeared to occur in 1957 and 1958, with another minor peak early in 1959. An examination of the area in the fall of 1959 showed very little activity. It is likely that the danger of further damage is remote until there is another population irruption. The population buildup appeared to be localized, and limited mainly to places supporting a fairly large number of Great Basin wild rye (*Elymus cinereus*) plants (Figure 2). These large perennial grass plants furnished both cover and food to the mice.



FIG. 1. Bitterbrush girdled by *Microtus*.



FIG. 2. Five-year old stand of reseeded bitterbrush plants which was protected from grazing by jackrabbits and cattle. The dark shrubs are bitterbrush and the bunchgrass is giant wild rye (*Elymus cinereus*).

TIME-MOTION STUDY OF A LIZARD¹

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A behavior pattern characteristic of lizards of the family Iguanidae in North America is the performance of push-ups or bobbing movements. As a part of a study of behavior in this family, a group of tree lizards (*Urosaurus ornatus*), collected in April from the Huachuca Mountains of southeastern Arizona, was observed during the summer of 1959 in an enclosure at the University of Oklahoma Biological Station, Marshall County, Oklahoma.

The enclosure measured 10 feet on a side and 3 feet in height and was constructed of sheet metal. The bottom was covered with fine sand piled up to an 18-inch dune in the center and 4 small logs and 10 hollow concrete building blocks (piled 2 high) were scattered at about 2-foot intervals throughout the enclosure. Many of the observations were recorded from a blind, but this would not have been necessary for the performance of the lizards; rather, it protected the observer from the hot sun. Other lizards present in this enclosure included species of the genera *Uta*, *Holbrookia*, *Sceloporus*, *Phrynosoma*, *Callisaurus*, and *Chemidophorus*.

The observations and measurements which follow concern 6 adult male and 2 adult female tree lizards that thrived in the enclosure from June 6 until August 14 when the observations were terminated. These tree lizards began to display within a few hours after they were released in the enclosure. Though all of them performed this display, social status determined the frequency of this activity (Carpenter and Grubitz, *Southwestern Naturalist*, 5:123) with the result that certain individuals contributed most of the data.

The display of the tree lizard consists of a sequence of push-ups in which the body, head, and tail are raised and lowered, all 4 legs being used about equally with each fully extended at the height of the push-up. The push-ups in the male are usually preceded by the lateral compression of the body, this compression partially exposing the ventral blue color of the male. The throat, which is also a deep blue or green in the male, is extended as a dewlap. The lateral compression and dewlap extension are maintained during the sequence of push-ups. The lateral compression and dewlap extension are not apparent during performance of the push-ups by the female. In displays by males performed specifically at another male, the performing male presents himself laterally to his adversary.

These displays were almost always performed on some raised object in the enclosure with the longitudinal axis of the body varying from the horizontal to vertical in position (head up or down).

The movements made during the display were of a specific type, following a predictable time-motion sequence. The number of push-ups varied with the intensity of the display, from as few as two weak push-ups to as many as nine vigorous push-ups. However, the time involved in each of these push-ups was consistent, and regardless of the number of push-ups in a sequence, a specific time-pattern was followed.

To analyze this time-motion sequence, the following method and instruments were used. A standard stop watch, calibrated to 1/5 second, was used to record the timings, and, if necessary, a hand operated counter was used to keep a record of the number of push-ups. Using

these tools, the observer sat at the edge of the enclosure and timed the push-ups. Because of the small periods of time involved, these timings were cross-checked to gain a more accurate measurement of the time of each push-up, and also the time intervals between successive push-ups. Timings were taken of all possible units and sequences (unexplainably, 2 sequences were omitted, but have no effect on the results). The first push-up was timed separately, as was each push-up, also the time between the starting of the first push-up and the end of the 2nd, the time between the starting of the first and the end of the 3rd push-up, and similarly, 1-4, 1-5, 1-6, 2-3, 2-4, 2-5, 2-6, 3-4, etc. (see Figure 1). The junior and senior authors made independent observations, which were later compared and compiled. The means for each timing by each observer differ by less than 0.1 second for 16 of 19 timings.

With such data at hand, we were then able to calculate the means for each timing and to construct a time-motion chart of the display. Early observations had indicated 6 successive push-up as the typical and most consistent number performed during display, so that most timings were based on this number.

Fig. 1 is for the dominant male of the group which was the most active and provided the largest number of timings (320).

The resulting time-motion pattern was as follows: The first push-up took one second, the second 1.5 seconds, the 3rd and following push-ups approximately 0.8 seconds each. The intervals between push-ups varied noticeably; 0.7 seconds between the first and 2nd and the 2nd and 3rd push-up, 0.3 seconds between the 3rd and 4th and the 4th and 5th, and 0.6 seconds between the 5th and the 6th. The 2nd push-up was conspicuously longer than the others, while the 3rd and successive push-ups were shorter than the first. The interval time between the 3rd and 4th push-ups was markedly shorter and appeared as a quick "kick-up."

The time-motion pattern of push-ups was consistent for all individuals observed within a degree of difference of less than 0.2 to 0.3 of a second, which would be accountable to human error. If 5 or 6 push-ups were performed, they followed the pattern described. If, as was observed a few times, the number of push-ups in a sequence was 8 or 9, the first 6 followed the pattern described with the remainder being the same as the 6th, though usually less pronounced. These less pronounced push-ups are termed weak, because the lizard did not raise up its full height. Infrequently, a male would perform one or 2 weak push-ups and then stop, however, these weak push-ups showed the respective time-motion pattern of longer sequences.

The push-ups performed by the females were less intense than those of most males, but otherwise their timings and sequences were the same. They averaged fewer push-ups per sequence than the males and did not show lateral compression, dewlap extension, or lateral presentation.

The time-motion pattern presented here is variable in tenths of seconds, but is consistent in the relative lengths of time for consecutive push-ups. This display pattern has been observed both in the field and in controlled populations, and is presented as a species-specific behavior pattern for the tree lizard (*Urosaurus ornatus*).

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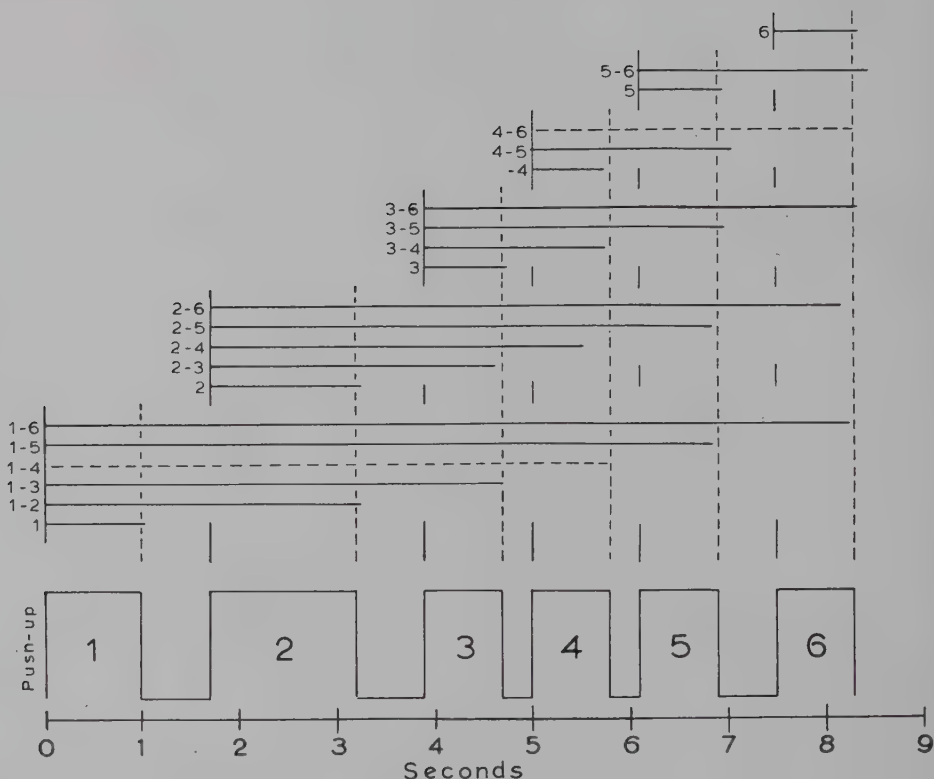


FIG. 1. The time intervals involved for each push-up and for intervals between push-ups, for a typical sequence of six push-ups in the display of the tree lizard *Urosaurus ornatus*. Bottom line is time in seconds. The pattern graph for six push-ups was determined from the plotted timings above.

THE MOVEMENT OF DISPLACED GREEN SALAMANDERS¹

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Previous studies of the green salamander, *Aneides aeneus* Cope, have revealed that the spatial movement of marked individuals is restricted (Gordon 1952, Tables 3A, B and C). Of 21 marked salamanders (excluding 6 females guarding eggs) recaptured at least once, only 4 moved more than 8 feet between point of release and point (or points) of recapture. Of 6 males captured at least 3 times (Male No. 2 was captured twice in 1950, not once as is indicated in Table 3A, Gordon *op. cit.*), 2 showed no movement between points of capture and 4 moved an average of 3.2 feet (extremes 2-6).

The data suggest a small home range with occasional individuals making dispersal movements. The whereabouts of marked individuals between dates of recapture were unknown. The habitat of this species (rock crevices,

¹ This research was supported by a National Science Foundation grant-in-aid administered by the Highlands Biological Station.

produced by fracturing and weathering, frequently deeply penetrating and anastomosing) is not conducive to the capture of every animal observed. The method of capture involves the insertion of a wire into the crevice and behind the salamander. Sometimes much prodding is required before the salamander moves out of the crevice and often a rapid retreat results in no capture. Thus I frequently could record only the presence of an adult or immature individual, without knowledge of its exact identity, in a crevice in which a marked individual was observed repeatedly on previous censuses.

The movements of adult females are highly restricted during most of the active portion of the annual cycle. The females remain in the breeding crevices from the onset of oviposition to hatching of the eggs, a period varying from 84 to 91 days (5 females observed, Gordon 1952). This guarding behavior of the female offers an

opportunity to test for the existence of a homing instinct in a completely terrestrial species.

METHODS

The displacement experiments were conducted in 2 populations, June 13 to July 2, 1959, at Granite City, Jackson Co. and Highlands, Macon Co., North Carolina. These are the same populations studied in the work reviewed above. Only those females occupying shallow crevices from which the salamanders could be removed with a minimum of trauma were used. Each female was removed, toe-clipped and replaced 24 hours before beginning the actual experiments. Because of the limited number of workable females (4), the displacement experiments (13 total) were designed to gather evidence for ability to home. Three females were removed to crevices on the same rock outcrop; the 4th was moved to crevices on different outcrops. Observations of their positions were made at 24 hour intervals unless noted otherwise. The limitations of time and number of females indicate the preliminary nature of these investigations.

RESULTS

The initial displacement of each female was followed by return to its respective breeding crevice within the 24 hour lapse between observations, from distances varying from 14 inches to 15 feet (Table I). In subsequent trials the return was delayed in 3 instances and one animal was lost.

TABLE I. Summary of homing movements of 4 female green salamanders, *Aneides aeneus*

Female No.	Date Moved (Time)	Distance	Date Returned (Time of Observation)	Remarks
1	13 VI (1000)	14 in	14 VI (0930)	Crevices on same outcrop. Spontaneous pattern of movement occurred from 16 VI to 25 VI.
	14 VI (0930)	14 in	16 VI (2130)	
	25 VI (2215)	24 in	—	
2	24 VI (2130)	5 ft	25 VI (2215)	Crevices on same outcrop.
	25 VI (2215)	5 ft	1 VII (2000)	
3	25 VI (1500)	14 ft	26 VI (0930)	Crevices on same outcrop.
	26 VI (0930)	14 ft	27 VI (1015)	
	6 VII (1615)	14 ft	7 VII (0900)	
	7 VII (0900)	14 ft	11 VII (2000)	
				Crevices on separate outcrops:
4	25 VI (1530)	15 ft	26 VI (1000)	5 in. crevass.
	26 VI (1000)	15 ft	27 VI (1015)	3 ft crevass.
	6 VII (1700)	16 ft	7 VII (0930)	5 in. and 4 ft crevass.
	7 VII (0930)	29 ft	8 VII (0915)	

Female 1, removed a second time on June 14, was not visible in any of the several crevices near the breeding crevice June 15, but was present in the displacement crevice on the afternoon of June 16. She was observed in the evening of the same day coiled beneath her eggs in the breeding crevice. Subsequent observations, June 17 through June 24, revealed a spontaneous pattern of movement on the part of the female between the breeding crevice where she spent each night and the displacement crevice used each day, a distance of 14 inches one way. On the evening of June 25 an attempt to interrupt this pattern was made, with the thought that a new pattern might be established. The female was moved to a 3rd crevice 24 inches from the breeding crevice. She was observed in the new displacement crevice at 0845 and

again at 2000 on June 26. Daily observations through July 4 failed to reveal her location. The prolonged absence of a female usually results in a steady loss of eggs from the clutch. The original 17 eggs were reduced to 5 by July 4.

Female 2 was inadvertently dropped (15 feet) during the displacement process of June 25. On June 26 the female was in the displacement crevice and did not respond with the usual escape movements when prodded with the wire. I returned the salamander to the breeding crevice. From June 27 through June 30, the female was not observed in the breeding crevice nor in any adjacent crevice. She was observed with the eggs at night on July 1 and at all subsequent visits to the area. No further studies involving this female were made.

Females 3 and 4 returned to their eggs upon repetition of the original displacement (Table I). The displacement of Female 3 was repeated July 6 with positive results. A 4th displacement occurred on July 7; however, considerable difficulty was experienced in removing the female from the crevice. A portion of the tail was broken in the process. Twenty-four hours later the female could not be found in either crevice nor in the several crevices adjacent to or between the breeding and displacement crevices. The female remained absent from the crevices until the night of July 11, when she was again seen with her eggs.

The displacements of Female 4 differed considerably from those of the other females. Basically the others were repetitions of the initial experiment. All 3 involved movement on the same rock outcrop. Female 4 was moved twice to the same crevice on an adjacent outcrop. The 2 outcrops were separated by a 5-inch crevass, the result of block faulting. The return trip involved either a jump across the gap which the salamander is capable of executing, or a detour of approximately 20 feet to the bottom of the gap and up the other side.

Since a return from the same displacement crevice each time could in itself involve a learning process, the 3rd and 4th displacements of Female 4 were varied. The 3rd removal was in an entirely different direction to a crevice on an adjacent rock outcrop. The straight line distance was 16 feet; however, in order to return to the breeding crevice, a gap of 3 feet had to be crossed and this involved considerable additional movement. The 4th displacement was in still another direction, a straight line distance of 29 feet to the breeding crevice, 2 outcrops away. Two crevasses, 5 inches and 4 feet had to be crossed in order to return. In all 4 displacements Female 4 returned to her eggs within the twenty-four hour lapse between observations.

DISCUSSION

During the period in which these experiments were in progress, rain occurred only twice, the nights of June 30 and July 10. The reappearance of Females 2 and 3, after absences of 5 and 4 days respectively, coincided with the occurrence of rain. Both occupied breeding crevices on outcrops which were much more exposed to insolation than those of Females 1 and 4. The displacement process prior to the disappearance of these 2 salamanders resulted in an unusual amount of prodding and handling which definitely aggravated water loss. Although this species can lose up to 30% of its body weight in water (Gordon 1952) and recover under experimental conditions, movement is definitely reduced after the first few minutes in the desiccation chamber. It is suggested that the same reduction in movement took place subsequent to displacement and that the salamanders returned only after reabsorption of surface moisture made available by the rain.

The movements of the displaced females imply a degree of orientation to (or familiarity with) the habitat which is not usually accorded urodeles. Noble (1931: 405) states that salamanders display a limited ability to learn a maze, but show no tendency to home. Twitty (1959), however, has provided ample evidence for homing in the salamandrid, *Taricha rivularis*.

It may be argued that the 24-hour lapse between observations is sufficient time for a salamander to reach the home crevice by trial and error. The return routes are unknown. Studies of locomotive periodicity in this species (Gordon, unpublished data) indicate that a major period of activity occurs between dusk and 11 P.M., with a minor peak approximately one hour before dawn. This would allow ample time for a salamander moving on one rock face to find its crevice. However, unless absence from the breeding crevice stimulates a longer period of activity, the 5 or so hours hardly seem sufficient to account for the movements of Female 4.

In view of the sedentary nature of this species, as evidenced by mark and release data, it is difficult to account

for the return of the females on the basis of familiarity with the habitat. Males, less sedentary than females, usually restrict their movements to the face of one rock outcrop and move relatively short distances on that outcrop. The movements of Female 4 clearly suggest a definite homing mechanism for plethodontid salamanders. Experiments designed to test the role of the various sensory organs of both males and females in orientation to the habitat are anticipated.

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MOUNDS OF THE ANT *FORMICA ULKEI* AT THE EDWIN S. GEORGE RESERVE, LIVINGSTON COUNTY, MICHIGAN¹

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INTRODUCTION

Formica ulkei Emery, an ant of the northern Midwest which builds large, conspicuous, cone-shaped mounds, has been much studied at Palos Park, Illinois, by students at the University of Chicago (Holmquist 1928, Dreyer and Park 1932, Dreyer 1942, Scherba 1958). This paper concerns, first, the local ecological distribution of the ant at another place, the Edwin S. George Reserve, Livingston County, Michigan, and second, its vigorous spreading into a newly opened suitable habitat along a recently constructed road.

The Edwin S. George Reserve is composed of 2 square miles of varied topography and habitats. It has dry upland fields and low, wet ones, deep oak-hickory woods and a variety of woods-border ecotones. There are ponds, marshes, swamps and bogs with diverse types of margins. The soil is basically a sandy-loam clay which dries out rapidly so that most of the habitats that are not near water are fairly dry.

DISTRIBUTION

A survey made it quite clear that in this environment *Formica ulkei* is definitely associated with water. Holmquist (1928) has stated that, at Chicago, nest burrows extend down to the soil water level. At the Reserve, this is possible only near bodies of water. A second requirement seems involved in keeping nests near water, that of aphid-harboring plants. *Formica ulkei* workers forage actively for dead insects, but their chief food seems to be the secretions of aphids. These insects can be found on some upland plants, but they are most common on shrubs that grow at the margins of swamps and marshes. Chief

among these are red osier dogwood (*Cornus stolonifera* Michx.), silky dogwood (*C. obliqua* Raf.), meadow-sweet (*Spiraea alba* Du Roi) and dwarf willow (*Salix* sp.). *Formica ulkei* workers commonly forage upon these plants.

Perhaps an account of places where *F. ulkei* colonies are not present will make clearer the requirements mentioned above. The ants cannot tolerate shade; therefore they are excluded from woods, even those bordering water. They are not found on high, dry fields, although aphid-harboring plants may be present there. They are not found on low ground which is subject to spring flooding, and they are not found in areas where aphid-bearing plants are absent. Thus *F. ulkei* mounds are most likely to be on banks above water in places where *Cornus* shrubs are abundant.

In spite of these restrictions, *F. ulkei* colonies are fairly numerous and widespread on the Reserve. They are found around several holes in Southwest Field and along the borders of Big Swamp, East Marsh, Fishhook Marsh, West Marsh, and Southwest Swamp. One hundred twelve such mounds were discovered in a survey made in 1958. At 3 places the mounds were especially numerous; 21 were located along the road built between Fishhook Marsh and Southwest Swamp, 12 along a road bordered on both sides by Big Swamp, and 24 around the depressions in Southwest Field. These 3 places were not alike, but had 2 characteristics in common: nesting places near water, but in no danger of being flooded, and the presence of aphid-bearing shrubs of the genus *Cornus*.

The nests in Southwest Field surrounded 2 large, abrupt depressions which were always moist and often had standing water in them. They were filled with tall black oak (*Quercus velutina* Lam.), willow (*Salix* sp.) and large-toothed aspen (*Populus grandidentata* Michx.), and were bordered with a dense growth of *Cornus* and other shrubs. The ant mounds were near the depressions, but were

¹ The work was assisted by a grant from the Edwin S. George Reserve scholarship fund. Facilities of the Reserve were made available by Dr. T. H. Hubbell, Acting Director, and Dr. Irving J. Cantrall, Curator of the Reserve.

out in an open field which was low and moist enough to support a dense growth of field plants. Conspicuous among these were blackberries (*Rubus allegheniensis* Porter), goldenrod (*Solidago* sp.), common milkweed (*Asclepias syriaca* L.) and bergamot (*Monarda fistulosa* L.). Grasses were primarily a mixture of Canada bluegrass and Kentucky bluegrass (*Poa compressa* L. and *P. pratensis* L.).

The road across the edge of Big Swamp had wide shoulders which were excellent places for ant mounds. Trees, such as black oak, large-toothed aspen, willow and tamarack (*Larix laricina* (Du Roi) K. Koch), were scattered enough to allow considerable sunshine. Shrubs filled the swamp edge on each side of the road. In addition to the *Cornus* there were dwarf willow, swamp birch (*Betula pumila* L.), shrubby cinquefoil (*Potentilla fruticosa* L.) and meadow-sweet. Shoulders were covered with grasses and *Equisetum* interspersed with patches of red raspberry (*Rubus ideaus* L.) and Indian hemp (*Apocynum cannabinum* L.) and a few scattered field plants such as the common milkweed.

The road between Fishhook Marsh and Southwest Swamp was somewhat more shaded and not quite so wide. Its trees were black oak (*Quercus velutina* Lam.), white oak (*Q. alba* L.), large-toothed aspen, elm (*Ulmus americana* L.), red maple (*Acer rubrum* L.) and black cherry (*Prunus serotina* Ehrh.). Again *Cornus* shrubs were thick at the water's edge, and the shoulders were covered with Canada and Kentucky bluegrasses and *Equisetum*, plus a variety of field forbs. This group of mounds was the one selected for a 6-year study of nest formation.

MODIFICATION OF PLANTS ABOUT MOUNDS

No matter where nests were located, the ants showed a distinct tendency to keep vegetation cleared around the mounds, an activity which seemed to keep the mound free from shade and was most successfully carried out by large, thriving colonies. The clearing was especially conspicuous in the fields, where ants would sometimes maintain almost pure stands of Canada or Kentucky bluegrass for 15 to 25 inches around the mounds in the midst of thick stands of tall blackberry bushes or other field plants. Ants near marshes and swamps seemed equally successful in eliminating small woody plants of *Cornus*, meadow-sweet, shrubby cinquefoil, dwarf willow and swamp birch. Overhanging branches of trees could not be controlled.

SIZE OF MOUNDS

The Chicago workers have adopted a method of expressing the size of mounds in terms of greatest diameter: medium sized nests measure 18 to 36 inches, small nests, less than 18 inches, and large nests, more than 36 inches. The 112 mounds at the Reserve in 1958 fell into the following categories: 51 large, 47 medium, and 14 small. Thus 45.5% are large, 42.0% medium and 12.5% small. This is close to the percentage which Scherba (1958) found in his 1954 survey of the Chicago mounds. The largest nest on the Reserve was an unusually elongated one measuring 180 inches long, 96 inches wide and 30 inches high. The next two largest mounds had the typical cone shape and were 96 × 84 × 34 inches and 95 × 75 × 26 inches.

COLONY FOUNDING

Formica ulkei has 2 methods of starting new colonies. By the first, a female may gain entrance into a *F. fusca* nest and begin her colony by means of temporary social parasitism. This method of colony founding was postulated long ago by W. M. Wheeler (1910). Years later, in 1933, Creighton (1934) found a single female which had been adopted by a small colony of *F. fusca* in North

Dakota. Evidently successful mixed colonies of *F. ulkei* and *F. fusca* are rare, for Scherba (1958) reported that none had been discovered in the Chicago area. One such colony was found on the E. S. George Reserve in 1958. The mound was typical of *F. fusca* in shape and was located at the weedy ecotone between marsh and field. It was completely covered by dense Canada blue grass, a sign that the colony was not thriving. This was verified when the mound was cut into, for only one side of the mound was being used. There were about equal numbers of *F. ulkei* and *F. fusca* workers. Both species carried larvae and pupae deeper into the nest when it was disturbed. A year later all of the *F. fusca* were gone, and the mound contained a thriving young colony of several hundred *F. ulkei* workers, together with a normal number of larvae and pupae. The mound still had the *F. fusca* appearance, and the *F. ulkei* colony occupied only one third of it. This method of colony-founding can account for the occurrence of isolated colonies.

The second method of establishing colonies accounts for the large clusters of mounds characteristic of some places. Scherba (1958) gives a good account of the establishment of new nests by budding from old ones. By this method groups of workers from the old nest proceed to build a new mound nearby. Larvae and pupae are transported from the parent nest and, presumably, fertile females are lured or pulled into the new nest sometime later. According to Scherba, soil that has been loosened or at least cleared of the plant cover is favored as a site for such new mounds.

COLONIZATION OF A NEW FAVORABLE HABITAT

This forming of new mounds by budding offers an effective method of the rapid colonization of any newly formed favorable habitat. At the Reserve such a habitat came into existence in the fall of 1950, when a new road of gravel and soil was built upon the old low road between Fishhook Marsh and Southwest Swamp. Since there were already large colonies of *F. ulkei* in the field bordering these bodies of water, the new road gave a suitable environment for expansion. By 1953 small mounds were numerous enough along the shoulders of the road to be conspicuous, and in August of that year they were first counted and measured.

Approximately 175 yards of the road extended across the low land between swamp and marsh, from a field on the east to a woods on the west. This new road seemed ideal for *F. ulkei* expansion in that it provided good banks which would not be flooded but which would allow the nests to extend down to water level, raw soil not already covered with dense vegetation, openings through the trees where sunlight could strike for at least part of the day, and a great abundance of aphid-bearing *Cornus* shrubs in the water on both sides of the road.

Only 3 of the 21 nests found along this strip in August, 1953 could have been present before the road was built, for all the rest were constructed upon the shoulders of the new road. Two of the 3 were situated at the west end of the swamp where the road rises into Southwest Woods. One of these (No. 4) was a beautiful large cone 99 × 90 inches in diameter and 25 inches high, with a good circle of cleared vegetation. This was a "parent nest." The one near it (No. 3) was smaller, 29 × 22 × 8 inches, and was probably a subsidiary nest formed by some previous budding. The 3rd mound (No. 15) was near the east end of the road. Unlike the others it was located 7 yards back from the road on a strip of land which extended out into the swamp. This was the large, elongated mound mentioned previously. The colony kept clear of shading vegetation a diameter of about 7 feet around the nest, but

beyond this it was surrounded by trees and shrubs. It seems probable that the 2 large mounds (Nos. 4 and 15), standing about 100 yards apart, gave rise to the 18 smaller nests found along the road in 1953. Since colonization seems to occur mainly in spring and early summer, none of these nests could have been more than 2½ years old, and some probably no older than one or two months. Their newness was indicated by their size, 5 being medium and 13 small. Many of the latter were exceedingly small. Two had no height, but were merely areas of many openings. The smallest measured $6 \times 10 \times 0$ inches. None of the small nests was more than 4 inches high, and the medium nests measured only 2 to 6 inches high. All of these seemed to give a picture of a vigorous expansion into a newly created favorable habitat by a process of migration from old colonies.

Certain questions naturally arose. How permanent were the new mounds? How many could ultimately be supported along the road? How long would occupants of new mounds stay in contact with the parent colony? To answer some of these questions, mounds were recorded and measured in late June and again in late August for each of the next 6 years.

The 6-year study showed quite clearly that many new mounds were formed and then abandoned, and that most of them had a very short existence. Worker ants were constantly moving up and down the road shoulders in great numbers, and evidently would gather and dig at any place which seemed favorable. Many of these little mounds did not survive the winter. Some formed in June were already abandoned by August. (Colonization was not completely limited to early summer, for some were found in August which had not been present in late June.)

Over the 6-year period, 56 mounds had been built. Of these 25 lasted less than a year, 13 lasted one year, one lasted 3 years, 4 lasted 5 years, and 13 were still present in August of 1959. Nine of the surviving 13 had been among the original 21 counted in 1953 (of which all but 3 must have been formed in 1951, '52, or '53). Thus the mounds built during the early years of colonization survived better than those formed later. Of the 4 younger mounds, built since 1953, one was 5 years old, 2 were 3 years old, and one was 2 years old.

Table 1 gives a summary of the numbers of mounds added each year, the number abandoned and the number present each year.

TABLE 1. Mounds of *Formica ulkei* added or abandoned each year during a period of colonization of a newly opened habitat

Year	Mounds added	Mounds abandoned	Mounds present
1953.....	—	—	21
1954.....	12	8	25
1955.....	5	12	18
1956.....	10	2	26
1957.....	6	6	26
1958.....	2	5	22
1959.....	0	9	13

It will be noted that numbers of mounds reached a peak in 1956 and 1957, and that by 1959 colonization seemed to have come to a standstill. No new mounds were found either in June or in August of that year, and 9 mounds had been abandoned since the year before. It seems probable that by another year the number of mounds will have dropped to 11, for 2 of the surviving ones are

small, overgrown with plants, and have very few openings. Perhaps the population will stabilize at that number, since the remaining mounds are medium to large and all seem flourishing. The road shoulders are no longer as open to mound construction as before, being thickly overgrown with tall plants and shaded by overhanging branches in more places.

The change in the numbers of mounds in the 3 size groups is another indication that colonization is coming to a standstill. In 1953 only 2 mounds were large, 6 were medium and 13 were small. In 1958 five were large, 8 medium and 9 small. In 1959 four were large, 6 medium and 2 small. Thus there is a consistent tendency toward fewer and larger mounds.

It seems possible that nests formed by colonizing do not lose their connection with the "parent" mound or with each other. One bit of evidence for this was gathered in 1957. On June 30, many ants were seen carrying worker larvae away from Nest No. 4. They formed a loose pathway about 2 feet wide as they crossed the road, 150 to 175 workers passing a given line each minute. After the ants crossed the road they continued down its shoulders (straight across a small mound without disturbing its excavating workers) for 33 yards to Nest No. 9 (formed in 1953 or before). Here larvae were carried down numerous openings in each of the mound's 3 peaks. At the same time, back at Nest No. 4, a second trail was slanting across the road and progressing in the opposite direction to a nest (formed in 1954) 14 yards away. Here again larvae were being carried from the parent mound to the younger one, and workers were being carried in either direction. Transportation of larvae was seen again on July 1 and July 4 of 1957, but not later. This seemed a clear indication of intercommunication among at least 4 mounds which had existed as separate entities for 3 or 4 years. No way was found of discovering how far along the road this intercommunication extended. Nor was any colonizing seen from the large Nest 15, near the other end of the road.

Colony No. 4 was the only one along the "ulkei road" which produced winged ants. During the early years it had abundant flights of both males and females, but in 1957, 1958 and 1959 it was producing only males. None of the other mounds ever harbored any winged ants. This seems especially strange for the large No. 15 mound.

Lack of independence of mounds is shown in another way by the merging and separating of 2 mounds. In 1953 Nest No. 9, measuring $14 \times 8 \times 2$ inches, and Nest No. 10, measuring $30 \times 18 \times 6$ inches, were about 6 feet apart. Each grew, and by 1956 they had merged, forming a 3-peaked elongated mound $147 \times 29 \times 7$ inches. They remained together until August of 1958, when they were again separate and No. 9 measured $76 \times 24 \times 4$ inches while No. 10 was $39 \times 31 \times 8$ inches. In June of 1959 they were still 2 separate mounds with unexcavated soil between them. Thus the evidence points to the presence of huge colonies, each occupying an undefined number of mounds which are interconnected by movement of workers from one to the other.

SUMMARY

One hundred twelve mounds of the ant *Formica ulkei* Emery were found in the 2 square miles of the Edwin S. George Reserve, Livingston County, Michigan. All were near water and were associated with aphid-bearing shrubs.

One small mixed colony of *F. ulkei* and *F. fusca* gave added evidence that new colonies are formed by temporary social parasitism. A 2nd method of colony forming, by migration from old established nests, was studied for a period of 6 years along a newly built road. Each year

new mounds were constructed, and each year others were abandoned. Fifty-six mounds were counted in the 6 years. Twenty-one were present in 1953, a high of 26 was reached in 1956 and 1957, and by 1959 no new mounds were formed and the number had dropped to 13. It seemed probable that populations of the new mounds had never lost contact with those of the old ones.

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DIRECT AND FOOD-CHAIN UPTAKE OF CESIUM¹³⁷ AND STRONTIUM⁸⁵ IN BLUEGILL FINGERLINGS

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Since increasing use of nuclear energy will expose more and more aquatic environments to at least low concentrations of cesium¹³⁷ and strontium⁹⁰, having long physical half-lives, information regarding factors controlling their biological fates is urgently needed by the basic and applied sciences which are concerned with these isotopes in natural systems.

Cesium and strontium are respectively chemically similar to potassium and calcium and may be expected to enter the solute complex, engaging in ionic antagonism. How-

ever, high concentrations of K and Ca were found not to interfere, respectively, with the selective uptake of Cs¹³⁷ and Sr⁸⁵ by many nonliving organic materials in laboratory trials. In living materials, however, such as green algae (*Cladophora*, *Pithophora* and *Euglena*) and bluegill fingerling fish (*Lepomis macrochirus* Rafinesque) when concentration was through a differentially permeable membrane K and Ca did respectively reduce the accumulation of Cs¹³⁷ and Sr⁸⁵. The addition of Ca when the concentration of K was high at 100 mg/l resulted in an

TABLE I. Bioaccumulation of cesium¹³⁷ and strontium⁸⁵ directly from water and by way of the *Euglena*-*Daphnia* food chain into fingerling bluegill fish

Source of radioactivity	Amount of radioisotope available, counts/min/gm or ml.	By <i>Euglena</i>		By <i>Daphnia</i>			By 8 BLUEGILL FISH		
		Uptake in 48 hours, c/min/gm	% retention after 48 hours in distilled water	Grams in-gested	Uptake in 48 hours, c/min/gm	% retention after 48 hours in distilled water	Grams in-gested	Uptake in 48 hours, c/min/gm	% retention after 48 hours in distilled water
Cesium ¹³⁷ :									
Water 2,000 ml.	1,000	240,000	18	—	1,200	27	—	620	31
<i>Euglena</i> 1.0 gm.	240,000	—	—	0.5	30,200	25	—	—	—
Activity derived from ingesting <i>Euglena</i> :									
<i>Daphnia</i> 1.0 gm.	30,200	—	—	—	—	—	1.0	1,330	74
<i>Daphnia</i> 0.5 gm.	30,200	—	—	—	—	—	0.5	640	71
Activity in <i>Daphnia</i> from direct uptake from water :									
<i>Daphnia</i> 2.0 gm.	1,200	—	—	—	—	—	2.0	75	53
Strontium ⁸⁵ :									
Water 2,000 ml.	1,000	16,000	22	—	23,200	36	1.0	250	38
<i>Euglena</i> 1.0 gm.	16,000	—	—	0.5	3,400	58	—	—	—
Activity derived from ingesting <i>Euglena</i> :									
<i>Daphnia</i> 2.0 gm.	1,700	—	—	—	—	—	2.0	116	58
Activity derived by <i>Daphnia</i> directly from water :									
<i>Daphnia</i> 20. gm.	1,900	—	—	—	—	—	2.0	98	42

unexpected but significant reduction in the uptake of Cs^{137} by these live algae and fish.

Water fleas (*Daphnia magna* Straus) were made radioactive with Cs^{137} or Sr^{85} by 2 methods: (a) by direct uptake from the water in which they were placed for 48 hours or (b) by depriving them of food for 48 hours and then allowing them to prey on the green flagellate *Euglena gracilis* Klebs which had been made radioactive by culturing in a nutrient medium containing Cs^{137} or Sr^{85} . Bluegill fingerlings were made radioactive with Cs^{137} or Sr^{85} by direct uptake from water and by feeding on *Daphnia* (Table I).

In each test 8 bluegill fingerlings averaging 2.1 grams were used. Two fish were added to 2 liters of water making 4 containers for each group of 8 fish. All tests were conducted in a constant temperature room at 25° C. A prepared soft water of 95 parts of distilled, demineralized water to 5 parts of natural spring water giving a total hardness of 20 mg/l as $CaCO_3$ was used in these cesium studies. In the strontium experiments tap water run through activated carbon and spring water were mixed to give a Ca-hardness of about 100 mg/l. All fish were starved for 48 hours before being fed *Daphnia*. Each fish was analyzed for whole body activity by means of a scintillation well-type detector connected to an integrating decade scaler. Following each gamma measurement the fish were returned to water free of these radionuclides.

All of the *Daphnia* were eaten by the fish within 18 hours. Feces were removed at about 10-hour intervals to minimize direct uptake from the water. After 48 hours the distribution of the cesium ingested by the bluegills was analyzed. Bluegills getting cesium from the *Euglena-Daphnia* food chain retained at this time about 72%, while the collected feces had about 15%.

Four fingerlings survived gamma analysis at 48-hour intervals for 20 days, each time being returned to water free of Cs^{137} . The loss of activity appeared to be exponential for the first 4 days (Fig. 1). At the end of 20 days, however, the count was 1,050, which is about 8% of the highest activity accumulated.

It is known that fish may take up cesium or strontium by ingestion and directly from solution. However, Krumholz and Foster (1957) report that the principal mode of accumulation of radiomaterials by fishes is through ingestion. In these studies bluegills accumulated Cs^{137} and

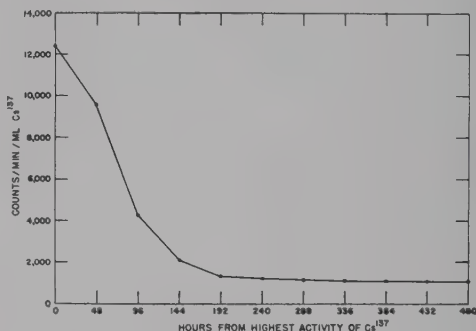


FIG. 1. Four bluegill fingerlings averaging 2 ml of displaced water were fed *Daphnia magna* made radioactive by feeding on *Euglena gracilis* which was radioactive from growing in a culture dosed with cesium¹³⁷. Each fish was whole body gamma counted in a tube containing 2 ml of distilled water at 48-hour intervals for 20 days. The fish were fed nonradioactive *Daphnia* every 72 hours.

Sr^{85} both ways during the 48-hour periods; however, at the 3rd trophic level from the *Euglena-Daphnia* food chain they showed higher concentration and retention factors for Cs and Sr than when accumulation was only from solution in 48 hours. It should be noted from Table I that *Daphnia* took up more Sr than Cs from solution.

Apparently some of these radionuclides, which have been taken up by *Euglena*, are bound to a chemical mechanism. This bound condition enables them to pass along a food chain through *Daphnia* into bluegills. Thus, higher concentrations and retentions of these radionuclides were obtained from the food chain route than from solutions in which the organisms were submerged.

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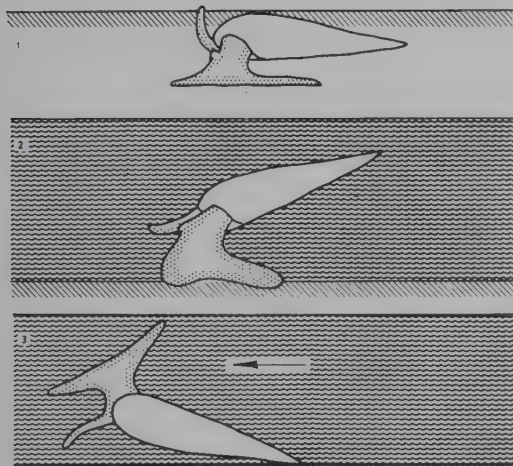
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OBSERVATIONS ON THE BEHAVIOR OF THE LITTORAL
GASTROPOD *TEREBRA SALLEANA*

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Terebra salleana Deshayes, a small, slender, high-spined gastropod measuring about 5 cm at maturity, is a common occupant of the intertidal zone on the Gulf of Mexico beach of Padre and Mustang Islands, Texas. According to Abbott (1955, p. 267), the range of this species is



FIGS. 1-3, Sequence of movements of *Terebra salleana* in regressing swash zone. Fig. 1, Snail burrowing in sand with only siphon exposed. Fig. 2, When sand is covered by swash water, the snail crawls to surface and raises the apex of its shell. Fig. 3, By throwing the apex to one side, the snail turns over on its back and, with the foot acting as a sail, glides seaward.

"North Florida to Texas and Columbia." Like other sand-burrowing snails, *T. salleana* has a large foot with which it ploughs through the sand. The foot of *T. salleana* is also used as a "sail" to enable the animal to move rapidly into deeper water when it is about to be stranded above the swash zone by a falling tide.

As the water recedes during a falling tide, the swash zone moves seaward and the interval of time between successive inundations of a previous swash zone becomes progressively longer. Specimens of *T. salleana* inhabiting an area being left behind by receding water remain below the sand with only the tip of the siphon exposed (Figure 1). Then, when a wave with more than normal force pushes swash water over the area each snail moves rapidly to the surface, raises the apex of the shell in a jerking movement (Figure 2) and, forcefully throwing the apex to either the right or left in a twisting motion, falls on its dorsal side with the foot facing upward; the foot, held at about a 45 degree angle to the longitudinal axis of the shell, now acts as a sail, and carries the snail seaward with the outgoing swash (Figure 3). With the foot in this position, *T. salleana* can be carried a considerable distance by a slowly moving current. This peculiar adaptation of the foot has not, so far as I know, been previously described.

Although insufficient data is available to more than speculate as to what motivates *T. salleana* to leave the sand when the changing tide leaves it behind, a hypothesis that suggests itself is that *T. salleana*, preferring a substrate frequently wetted, climbs out of the sand into the swash water whenever the intervals between inundations become too long.

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CORRECTING BEHAVIOR IN BOXELDER BUGS

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INTRODUCTION

For 6 years freshman zoology classes at the University of Michigan have been using boxelder bugs (*Leptocoris trivittatus* Say; Hemiptera, Coreidae) for behavior studies. The type of behavior studied, I have here designated "correcting behavior." A bug is made to run along a causeway for a certain distance. The causeway then makes a 90° turn, the bug again running a given distance before being presented with a choice of either making a 2nd turn so as to be headed in the original direction or continuing straight ahead. If the bug makes the turn at the choice point thus ending the run facing in the same direction as when it started, it is said to, "correct." Similar phenomena have been observed in ants (Schneirla 1929), cockroaches (Hullo 1948), rats (Dashfield and Bayroff 1931, Ballachey and Buel 1934, and Witkin and Schneirla 1937), and even in children (Gellerman 1931).

The procedure used by the students of the freshman classes is quite simple. They construct causeways of plasticene and place them in pans of water which usually prevents the bugs from stepping off. Care must be taken to keep the walking surfaces dry, for once a bug gets wet, the water becomes less effective in preventing it from stepping off the causeway. The bugs will move toward light and have in fact been observed to collect in areas of sunlight in the wild (Tinker 1952) and along the sides of their cages or jars nearest the window in my laboratory. The causeways are therefore oriented toward a window with the 2 possible final routes at an equal angle to the parallel rays of light; either route chosen by the bug takes it toward light, with the bug getting no advantage relative to light by making one choice or the other. By varying the distances between forced turn and choice point, students can observe changes in the fre-

quency of the correcting behavior. The research discussed in this paper is an attempt at critical analysis of this phenomenon.

I should like to thank Drs. R. D. Alexander, Morris Foster, and R. W. Gerard for reading the manuscript and offering many helpful suggestions and criticisms and Dr. F. E. Smith for checking through the statistical methods. Special thanks are due to Dr. L. B. Slobodkin who has offered constant advice and criticism throughout the course of this research. To my wife, Geraldine Dingle, I am indebted in ways too numerous to mention.

METHODS

Instead of using plasticene, I made permanent causeways of wood and placed them in water. They were weighted at each end with a lump of plasticene and leveled by making sure that all along the causeway the walking surface was just above the water level. The walking surfaces were 6.5 mm wide which was just wide enough for one bug to walk. Several causeways were made, one T-shaped, but the others forcing the bugs to make one turn, travel a given distance, then make a choice between a straight path or a 2nd turn to correct for the first. The distance traveled by the bugs from the start to the forced turn was 15.0 cm unless noted otherwise; that between the forced turn and the choice point was varied. Causeways were initially waterproofed with

commercial plastic spray, and all corners were smooth. The light source used in all experiments was a window at one end of the laboratory with the pans containing the causeways on a table next to it (Figure 1).

In some experiments the bugs ran a single causeway 10 times in succession. In others they ran 3 different causeways one after the other and then were brought back to the first and the process repeated; the bugs ran each 3 or 5 times for a total of 9 or 15 trials per bug. While running, the bugs were timed for the distance between the start and the forced turn; the hesitation, if any, at the forced turn; and the distance between the forced turn and the choice point. No reward was given at the completion of a run; the bug was simply picked up, held by the experimenter, and then started again when the data from the previous run had been recorded.

ABILITY TO CORRECT

The first experiment in the analysis of correcting utilizes the data gathered from 72 "naive" bugs which were seeing a causeway for the first time. These bugs were run once on a causeway having a distance of either 1.25 cm or 3.75 cm between the forced turn and the choice point for a total, therefore, of 72 trials. Of these bugs 49 corrected and 23 did not. A χ^2 test on the data with a null hypothesis of a 1:1 ratio yielded $P < .01$; thus we can conclude that the bugs, although "naive," definitely do correct.

WINDOW

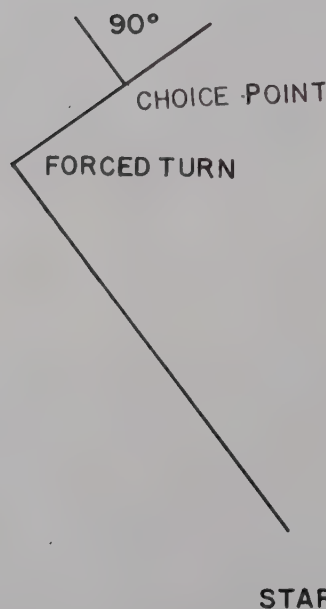


FIG. 1. Diagram of the apparatus used. The distance from the start to the forced turn was 15.0 cm in all trials. The distance between the forced turn and the choice point was varied. The two final routes were at an equal angle to the parallel light rays from the window.

TABLE I. Distribution of corrections made by 30 bugs when run 10 times in succession on a causeway with forced turn 15.0 cm and choice point 18.75 cm from start

Number of corrections	0	1	2	3	4	5	6	7	8	9	10
Number of bugs.....	—	—	2	—	2	3	1	4	9	4	5

In 2 other experiments I also determined the existence of correcting. In the first, 30 bugs were each run 10 times in succession over the same causeway with a distance of 3.75 cm between forced turn and choice point. The results are summarized in Table I. This observed distribution was compared with the theoretical distribution calculated from the binomial again assuming that the bugs stood an equal chance of correcting or not correcting. The test used was the two-tailed Kolmogorov-Smirnov one-sample test (Siegel 1956) which yielded $P < .01$. Hence the bugs show a highly significant tendency to correct.

In the 2nd experiment 10 bugs were run over a series of 3 causeways in succession, as indicated in the "Methods," of which the last had a distance of 3.75 cm between forced turn and choice point. The first 2 causeways had forced turn to choice point distances of 1.25 and 2.50 cm, respectively. In addition, 10 other bugs were run over 3 causeways of which the first had a forced turn to choice point distance of 3.75 cm and the last 2 had, respectively, 5.0 and 7.50 cm. The bugs were run 5 times per causeway for a total of 15 trials per bug. To test for correcting ability, I considered the 5 trials that all 20 of the bugs made on a causeway having a 3.75 cm forced turn to choice point distance. Three of the bugs are eliminated from consideration because of injury due to handling during the course of the experiment; the results for the remaining 17 are summarized in Table II. These, too, were compared with the binomial distribution making the same assumptions as above, and using the Kolmogorov-Smirnov test; the result was $P < .01$. Thus, here as well the bugs showed a significant tendency to correct. The effects of

different forced turn to choice point distances on correcting are discussed below.

TABLE II. Distribution of corrections made by 17 bugs run 5 times each on one causeway as part of a series of 15 runs on 3 causeways. Distances as in Table I

Number of corrections	0	1	2	3	4	5
Number of bugs.....	—	—	1	5	8	3

Two control experiments on correcting were run. The first utilized the T-shaped causeway to test whether or not the bugs actually do tend to go in the direction they start or will simply make any turn offered. The causeway was set up with the 2 destinations at an equal angle to the light from the window (Figure 2). The results of the sample of 11 bugs are summarized in Table III. I again used the Kolmogorov-Smirnov test comparing these results with the binomial distribution, and obtained $P < .01$ showing that the bugs do keep going forward and do not turn. The second control was designed to test for a possible bias in the system such as unequal distribution of light intensity which might influence the results. In this experiment the bugs were run 10 times in succession on a causeway which was then rotated 180° to reverse the 2 final routes. Here, to get to the same point it reached by correcting when the causeway was in the first position, a bug would have to go straight ahead after making the forced turn when the causeway was in the 2nd position (Figure 3). The bug was then run 10 times with the causeway in the 2nd position. The bugs made their first 10 runs alternately in the first and 2nd positions. Out of a sample of 10 bugs only 2 differed by as much as 3 corrections in the 2 positions, and the mean difference, taking sign into account, was $+0.2$. Using the two-tailed Wilcoxon matched-pairs signed-ranks test (Siegel 1956), I found $T = 20$ and $P >> .10$ indicating that there is no significant difference in performance due to rotation of the causeway. Any bias due to light or other factors which might be present in the system does not then seem to affect the course of the experiments.

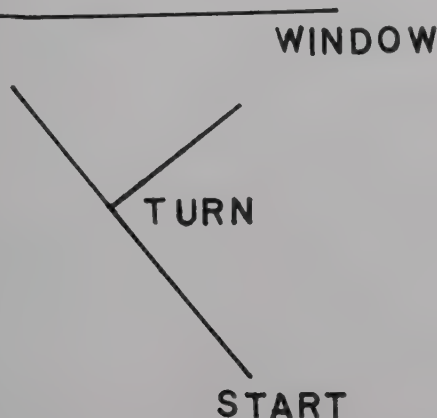


FIG. 2. Diagram of apparatus used in first control experiment. The distance from the start to the turn was 15.0 cm. The two final routes were at an equal angle to the window.

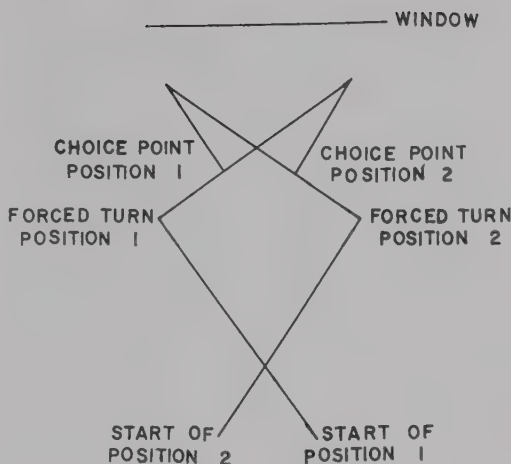


FIG. 3. Diagram of apparatus used in 2nd control experiment. Position 2 represents the causeway at Position 1 rotated 180° ; the end points are thus reversed. The distance from start to forced turn was 15.0 cm; that from forced turn to choice point was 5.0 cm.

TABLE III. Distribution of straight runs made by 11 bugs when run 10 times in succession on the control causeway shown in Figure 2. The distance of start to turn was 15.0 cm

Number of straight runs	0	1	2	3	4	5	6	7	8	9	10
Number of bugs.....	—	—	—	—	—	1	—	—	1	2	7

NYPHS VS. ADULTS

Thinking that there might be an age difference in the ability of the bugs to correct, I performed an experiment comparing 5th instar nymphs with adults using animals which had all been collected at the same time and place. Because of the lateness of the season (October), nymphs in earlier stages of development were not available in any quantity. A sample of 13 adults and 13 nymphs was run over 3 causeways having distances of 1.25 cm, 2.50 cm, and 3.75 cm between the forced turn and the choice point with each bug run 3 times on each causeway and 9 times in all. The results are shown in Table IV. Using a two-

TABLE IV. Distribution of corrections made by 13 adults and 13 nymphs in a series of 9 runs on 3 causeways with distances of 1.25, 2.50, and 3.75 cm between forced turn and choice point

Number of corrections	0	1	2	3	4	5	6	7	8	9
Number of adults	—	—	—	—	—	—	3	6	3	1
Number of nymphs.....	—	2	—	—	4	3	1	2	1	—

tailed Kolmogorov-Smirnov two-sample test, the 2 groups were compared with the conclusion that adults make a significantly greater number of corrections than the nymphs ($P = .01$).

TIME AND DISTANCE

The times it took 25 bugs to run given distances the first time they corrected and the first time they did not during the same series of trials were next considered. In no case did I find that the time it took a bug to travel a certain distance affected its tendency to correct. Using the 2-tailed Wilcoxon test, I found $P \gg .10$ for the time from the start to the forced turn, $P \gg .10$ for forced turn to choice point, $P \gg .10$ for hesitation at the forced turn, and $P \gg .10$ for total time. Therefore probability of correcting is apparently independent of time within the ranges tested for any portion of the run.

The behavior of the bugs between the forced turn and the choice point is, however, reflected in their rates of travel for that distance. With few exceptions they travel more slowly between forced turn and choice point than between start and forced turn. Table V gives the rates traveled on 15 runs by 15 different bugs chosen at random. With one exception the bugs proceeded more slowly between forced turn and choice point; using a 2-tailed Wilcoxon test, I found $P < .01$ showing real significance. Between start and forced turn the bugs move directly down the causeway with at most one or two slight hesitations while, between forced turn and choice point, they hesitate frequently. In a typical example a bug would move rapidly and directly down the first leg until it came to the forced turn. It would first start off the end and then sometimes start toward the choice point, but usually hesitate for a moment waving its antennae and front legs. After making the turn, it would hesitate, proceed slowly, and usually hesitate at least once again before reaching the choice point. Some bugs proceeded partially sideways for the first part of the distance between forced turn and choice point.

TABLE V. Rates of travel on runs by 15 different bugs chosen at random

Start to forced turn	Forced turn to choice point
1.88 cm/sec	0.94 cm/sec
3.76	3.75
2.14	1.88
5.00	0.94
1.88	0.75
3.00	1.88
2.14	3.75
2.50	1.25
5.00	1.25
1.00	0.23
1.50	1.25
5.00	1.88
2.14	0.63
2.50	0.94
1.88	0.71

The waving of the antennae at the forced turn does not seem to have an irreplaceable function in the ability of a bug to correct. I removed the antennae from 5 bugs, and the minimum number of corrections out of 10 trials made by any of them was 8. The bugs used, incidentally, were "naive" as defined above.

Although time of run does not affect correcting ability, distance traveled very definitely does. In 2 series of trials bugs were run for distances of 15.0 cm and 3.0 cm between start and forced turn with the distance between forced turn and choice point constant at 5.0 cm. The bugs corrected more often when they had a run of 15.0 cm before coming to the forced turn. Using a 2-tailed Wilcoxon

test, I found the average difference in corrections, taking account of sign, to be $+6.2$, $T = 0$, and $P \ll .01$. A reasonably long initial run would thus appear necessary for the behavior. Table VI gives the average rate computed from 10 runs that bugs traveled when going 15.0 or 3.0 cm between start and forced turn. A 2-tailed Wilcoxon test yields $P > .05$ showing that the difference is not significant. Furthermore, because of the difficulty of measuring accurately the time it took a bug to go 3.0 cm, the rates for that distance are underestimated. A more accurate estimate of these rates would have yielded a still higher P . I therefore feel safe in stating that there is no significant difference in average speed when running 15.0 cm or 3.0 cm from start to forced turn. Distance and not time is thus the factor which determines the behavior of bugs.

TABLE VI. Average rates for 10 runs of bugs traveling 15.0 and 3.0 cm between start and forced turn

Bug	Ave. rate 15.0 cm	Ave. rate 3.0 cm
R1.....	2.6 cm/sec	1.3 cm/sec
R2.....	2.6	2.1
R3.....	1.6	1.4
R4.....	3.3	2.5
R5.....	2.4	1.9
R6.....	1.5	1.9
Y1.....	0.77	1.1
Y2.....	2.5	1.4
Y3.....	2.1	1.7
Y4.....	2.2	2.5

Distance between forced turn and choice point was also a factor. In a series of trials, bugs were run 10 times for 3.75 and 7.50 cm for this distance with the distance between start and forced turn remaining at 15.0 cm. A greater number of corrections was made at 3.75 cm. Again using the 2-tailed Wilcoxon test, the average difference was $+3.0$, $T = 5$, and $P < .02$ indicating that ability to correct decreases with distance traveled down the 2nd leg. This conclusion was further substantiated by trials using 2 independent samples which are summarized in Table VII. In these trials one sample of 10 bugs was run on a causeway with 3.75 cm between forced turn and choice point and the other on a causeway with 12.50 cm between the 2 turns. Using the 2-tailed Kolmogorov-Smirnov test for 2 independent samples, $P = .05$, again indicating that correcting ability decreases with increasing distance between forced turn and choice point.

TABLE VII. Distribution of corrections made by bugs when run 3.75 and 12.50 cm between forced turn and choice point

Number of corrections	0	1	2	3	4	5	6	7	8	9	10
Number of bugs at 3.75 cm.....	—	1	—	—	—	—	2	1	2	4	—
Number of bugs at 12.50 cm.....	4	1	2	—	—	1	2	—	—	—	—

LEARNING

In those cases where bugs were run 10 times in succession on a single causeway, I considered the possibilities of "learning" or "habitation" (as the terms are defined by Thorpe 1951) as well as "fatigue." If there were learning, the number of corrections on later trials should be more

than on the earlier, with the converse true if there were habituation or fatigue. I considered the number of corrections made by 48 bugs on each of the 10 trials when they were run 10 successive times on a causeway. I found no significant difference in the performance of the bugs from trial to trial (using χ^2 , $P > .80$); therefore I have no evidence of learning, habituation, or fatigue.

DISCUSSION

Two possibilities appear at first glance to afford the simplest explanations of correcting behavior. The first would be an explanation based on purely physical grounds; the 2nd would be one based on some sort of conditioning mechanism due to reinforcement. Because of the 2nd control experiment, a bias in the system can be ruled out as a cause of the behavior. But another attempt at a physical explanation of the correcting phenomenon is the concept of "centrifugal swing" (Schneirla 1929 and 1933, Witkin and Schneirla 1937, Ballachey and Buel 1934).

The "centrifugal swing" theory was first put forth by Schneirla in his 1929 paper on maze running in ants. An ant, when it rounded a corner with sufficient speed, was "thrown" by its "momentum" against the far wall of the turn and proceeded along that wall until compensatory movements restored its "normal center of equilibrium." While under the influence of this "centrifugal swing," the ant easily made any movements which were compatible with it. While running along the far wall of the turn, the ant's head was so close that her antennae were almost doubled and her body nearly at right angles.

But "centrifugal swing," does not explain correcting behavior. With few exceptions hesitation occurred at the forced turn thus eliminating any momentum. Also, bugs arriving at the forced turn, regardless of whether they had traveled 3.0 or 15.0 cm to get there were traveling at roughly equal speeds (Table VI) and hence had about the same momentum. Under an hypothesis of "centrifugal swing" one would predict that the 2 groups would show the same number of corrections. However, the bugs traveling 15.0 cm from start to forced turn corrected more often.

If there were some sort of reinforcement for correcting in the system, the behavior might be considered a "Type II conditioned reflex" (Konorski 1948) or "trial and error learning" (Thorpe 1951 and 1956). However, I do not believe it can be considered as such. I think it very unlikely that there is any reinforcement since a Type II conditioned reflex should improve with successive trials. As we have seen, this is not the case, for the performance of bugs on the 10th trial is not significantly different from that on the first.

Apparently the correcting behavior of the bug must be "fixed" in some way while the bug is traveling from the start to the forced turn, and the degree to which it is "fixed" is a function of that distance, but is independent of the time it takes to travel over it. Once the bug has negotiated the forced turn, its "memory" is a function of the distance between that and the choice point and it fades more as the distance increases and a new direction becomes "fixed." This latter phenomenon is also independent of time within the ranges studied.

I should like to emphasize that the term "correcting behavior" is purely descriptive and implies no causative factors. A more comprehensive explanation must await further experiment.

SUMMARY

1. Boxelder bugs when forced to make a turn on a causeway will usually, if given the opportunity, make a 2nd opposite turn. I have termed this phenomenon "correcting behavior."
2. The correcting behavior of adults is significantly better than that of 5th instar nymphs.
3. Correcting ability is independent of the time it takes bugs to travel any of the distances on the causeway. However, decreasing the distance between start and forced turn reduces the ability to correct as does increasing the distance between forced turn and choice point.
4. When bugs were run on a causeway 10 times in succession, I noted no improvement in the 10th run over the first.
5. Because of the above, I have rejected an explanation based on a Type II conditioned reflex.
6. I have also rejected an explanation based on "centrifugal swing."
7. The term "correcting behavior" is for the present purely descriptive.

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A TIMING DEVICE SUITABLE FOR FIELD STUDIES UNDER ADVERSE CONDITIONS

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A simple, inexpensive, extremely sensitive, mechanical timer is herein described which has proved to be of value in determining the exact time at which an animal was trapped or had moved. This device is constructed from a mechanical alarm clock, a bobby pin, a one-pound coffee can with lid and some waxed fishing line.

Because of its low cost and simplicity, this timing device has obvious advantages over certain electronic techniques of timing although it has the disadvantage of not being suitable for repeated timings unless reset by the operator. This timer has been used successfully in deep snow and under rainy and icy conditions for trapping water shrews (*Sorex palustris navigator* [Baird]) in live traps near high mountain streams in Utah during a behavioral study by the authors.

The timer can be constructed from almost any mechanical 40-hour alarm clock although those with large balance wheels are preferable for quick and easy timer setting. The clock mechanism is first removed from its

case and, since it is to be placed face-down in a weather-proof can, paper clip legs must be attached to the sides of the face (see Figure 1) to suspend the clock so that the hands will not rub against the bottom of the can. A one-pound coffee can with a one-eighth inch hole drilled in the side at the level of the balance wheel is used as a covering for the timer.

The clock is fully wound and the balance wheel spring is then wound by turning the balance wheel 2 or 3 times which creates a spring tension which, when released, starts the clock. A bobby pin attached to a length of waxed fishing line is inserted through the hole in the can and clipped to the tense balance wheel. The other end of the string is then attached to a set trap or anchored across a runway, hole or nest, etc. The timer is now ready for operation.

The pre-wound clock is set at 12 o'clock and when the string is disturbed by an animal or the trap is sprung the bobby pin slips off the balance wheel and the clock begins to run. The exact time the mechanism was actuated can be calculated by subtracting the number of minutes the clock has run from the time of observance. Since the main-spring of the clock will expand at a constant rate, 12, 24 and 36 hour intervals can be determined by the degree of unwinding. Excess oil should be removed from the mechanism when used under cold conditions.

The timer can also be attached to two or more traps in series if experimental and control bait studies are desired. This can be accomplished by threading the line through the jaws of the snap traps and then attaching the line to the jaw of the terminal trap. Thus, when one of the traps is sprung, the line moves freely without affecting the other traps. When using live traps with fine mesh screen doors, the same effect may be achieved by attaching paper clips to the outer edge of each of the trap doors, excepting the terminal trap to which the line is tied. These paper clips allow the line to flow freely when one of the traps is sprung (Figure 1). Obviously, if animals are caught in more than one trap in the series, one cannot determine which trap was first sprung, so it is desirable to have separate timers for each trap.

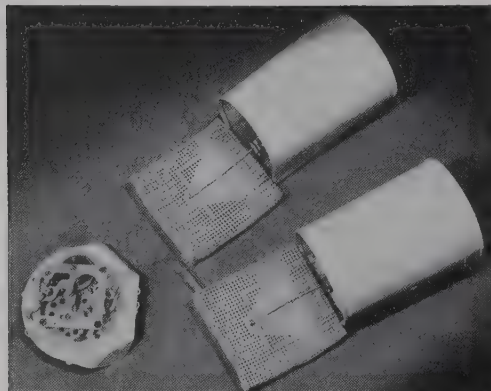


FIG. 1. Exposed timing device illustrating the positioning of the release mechanism on the balance wheel.

THE INFLUENCE OF TEMPERATURE AND ATMOSPHERIC PRESSURE ON THE RATE OF OXYGEN UPTAKE IN *TRIBOLIUM CONFUSUM*¹

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INTRODUCTION

Previous work of the author (1957) indicated that the rate of oxygen uptake in the flour beetle, *Tribolium confusum* Duval, was affected by changes in altitude and temperature. That temperature has this effect is well

¹ The support of the National Science Foundation under Grant G-4810 is gratefully acknowledged. The work of this report was carried out under the auspices of the Jackson Hole Biological Research Station, Moran, Wyoming. The interest and encouragement of Dr. L. Floyd Clarke, Director of the Research Station, is also gratefully acknowledged.

known for a wide variety of animals (Bullock 1955, Scholander 1953). The precise role of altitude in this apparent alteration of the metabolic rate is not so well understood. The experiments reported here were undertaken to explore further the nature of the change in rate of oxygen uptake which takes place with changes in altitude.

Tribolium confusum is not native to higher elevations in the United States. It seems reasonable to believe that it has not incorporated as a species physiological adjustments to the ecological complex of high altitude which native forms have developed. The extent of such adjustments to altitude are only partially known. Best known

are various aspects of the mammalian response to lowered oxygen pressure, a result of numerous studies stimulated by the problems of aviation medicine. Less well known are the responses of groups which do not compensate for changes in oxygen availability by changes in haemoglobin level. As an invertebrate, *Tribolium* is of particular interest in this context because of the relative lack of respiratory pigments (Wigglesworth 1950). This lack, along with a comparatively simple respiratory system would seem to provide a situation in which there is a closer adjustment between the organism and the surrounding atmosphere than exists, for example, in the mammals where an increase or decrease in the amount of haemoglobin present in the blood tends to compensate for changes in oxygen concentration over considerable ranges of altitude. It also seems reasonable to believe that in such a non-native organism the response to changes in the atmospheric pressure component of altitude, where other factors are held constant, is due to changes in gas pressure and not to prior adjustments to temperature or other unspecified or unknown factors.

MATERIALS AND METHODS

Larval stages of the beetle were selected as subjects for the following reasons: In a series of exploratory experiments (1958 unpublished) larvae of different ages were exposed to various combinations of temperature and altitude; the results suggested that the different age classes of larvae differed in their response to the conditions imposed; the large, nearly mature larvae usually survived while the small, very young larvae usually did not. Larval age or size, or both, appeared to play a role in determining the response of the organism.

For the present experiment 2 classes of larvae were selected, (1) large larvae of an average weight of 0.0028 grams each and (2) small larvae of an average weight of 0.0005 grams each. Both classes of larvae along with suitable controls were exposed to experimental treatments consisting of the 9 possible combinations of the following temperatures and altitudes:

T_1 —10° C	A_1 —sea level (simulated)
T_2 —15° C	A_2 —6750 feet altitude
T_3 —24° C	A_3 —14,000 feet altitude (simulated)

(Hereafter in this report T_1 , A_1 etc. will refer to the above temperatures and altitudes.)

A capillary tube 1.5 mm in diameter was used in making oxygen uptake determinations. A single larva was placed in the tube in such a way that the carbon dioxide excreted was absorbed by a potassium hydroxide solution. This occurs as the insect is utilizing oxygen from the tube which had been sealed by a movable oil droplet. The net change in volume occurring as a result of these 2 processes was read from a grid as the oil droplet moved across it.

Further details and a diagram of the apparatus used are given in an earlier paper by the author (Kennington 1957) and need not be repeated here.

The results of the experiment are summarized in Table I and illustrated in the accompanying figure.

RESULTS

Two well-known phenomena are evident. First, in all cases the smaller-sized larvae take up a proportionately greater amount of oxygen and, second, in all cases, an increase in temperature is correlated with an increase in oxygen uptake. A third feature is also evident. When temperature is held constant, an increase in oxygen uptake appears to result from an increase in altitude. Comparing only highest and lowest temperatures and highest and lowest altitudes, mean rates of oxygen uptake within and between larval groups are significantly different, in most cases highly so. The smallest difference, slightly over 2.5 times the standard error of the difference, occurred between the means corresponding to sea level and 14,000 feet altitude within the small larva class at a temperature of 15° C.

DISCUSSION

It is instructive to examine these results from the point of view of the gas laws of elementary chemistry and physics. The relation between the change in gas volume with pressure and the difference in rate of uptake with change in pressure can be shown by means of an example. The oxygen uptake of the large larva class, measured at 24° C between sea level and 14,000 feet, will be used as an example. Let the initial pressure $P_0 = 760$ mm Hg and the initial volume $V_0 = 1$. Then, in the example selected, $P_1 = 460$ mm Hg and $V_1 = x$. Applying the pressure volume formula $P_0 V_0 = P_1 V_1$, V_1 turns out to be 1.65, an increase of 0.65 cc per gram per hour. The increase in oxygen uptake found experimentally in the example cited here is 0.58 cc per gram per hour. It is apparent that the increase in rate of oxygen uptake from sea level to 14,000 feet is comparable to the change in volume of the atmosphere over the same range of altitude. This relationship is presented more fully in Table II.

Before discussing the results of the experiments on the relation of pressure to volume and rate of oxygen uptake, reference to similar experiments on the relation of temperature to volume and rate of oxygen uptake should be made. The rate of uptake of the large larva class measured at sea level between temperatures of 10 and 24° C will be used as an example. Calculations based on the temperature coefficient of expansion show that a rise in temperature of 14° C will produce an increase in volume of approximately .0514 units (Handbook of Chemistry and Physics). The change in rate of uptake found experimentally over the same range in the example cited is

TABLE I. Rates of oxygen consumption in cc per gram per hour for 9 combinations of temperature and altitude for large and small larvae of *Tribolium confusum*

Altitude	LARGE LARVAE						SMALL LARVAE					
	10° C		15° C		24° C		10° C		15° C		24° C	
	$\bar{x} \pm s$	N	$\bar{x} \pm s$	N	$\bar{x} \pm s$	N	$\bar{x} \pm s$	N	$\bar{x} \pm s$	N	$\bar{x} \pm s$	N
Sea level	.26 ± .16	24	.59 ± .13	10	1.44 ± .44	17	.89 ± .44	22	1.23 ± .54	7	2.81 ± 1.11	37
6750 feet	.36 ± .11	29	.88 ± .70	25	1.91 ± .89	44	1.10 ± .56	20	1.83 ± 1.21	19	4.21 ± 1.22	20
14000 feet	.56 ± .19	15	1.02 ± .37	27	2.27 ± .84	16	1.82 ± 1.01	17	2.03 ± .84	18	6.58 ± 2.10	19

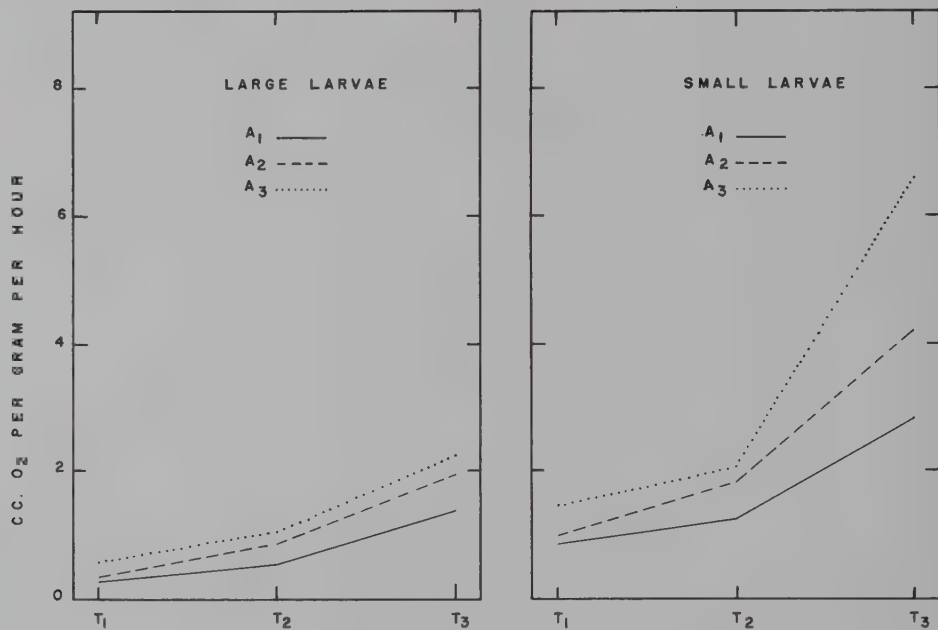


FIG. 1. Graphs showing rates of oxygen uptake for various combinations of temperature and altitude.

TABLE II. The relation between increase in atmospheric volume with change in altitude and apparent increase in rate of oxygen uptake in large and small larvae of *Tribolium confusum*

Conditions being compared	Factor of increase in atmospheric volume	FACTOR OF INCREASE IN RATE OF OXYGEN UPTAKE					
		10° C		15° C		24° C	
		Small larvae	Large larvae	Small larvae	Large larvae	Small larvae	Large larvae
Sea level to 6750 feet	1.27	1.49	1.38	1.24	1.33	1.14	1.49
6750 feet to 14000 feet	1.30	1.16	1.55	1.65	1.19	2.06	1.11
Sea level to 14000 feet	-1.65	2.04	2.14	1.65	1.73	2.34	1.58

$1.44 - 0.26 = 1.18$ cc oxygen per gram per hour, a 25-fold difference. This result leaves little doubt that the increase in oxygen uptake that accompanies an increase in temperature is not a simple result of the expansion of the atmosphere caused by temperature.

These results indicate that the organism is able to maintain an approximately constant rate of oxygen use in the face of falling pressure. The apparently greater volume of oxygen used at the lower pressures reflects the larger amount of space which the same number of molecules occupy at the lower pressure. On the other hand, the nature of the adjustment to temperature seems to be quite different. The physical expansion of the gas due to temperature is too small to account for the rise in oxygen uptake on the hypothesis that the organism is using the same number of molecules from a larger space. This hypothesis, on the other hand, will account for virtually

all of the change in rate of uptake which accompanies a change in atmospheric pressure.

On a molar basis, oxygen consumption remains relatively constant over the range of pressures tested. On the basis of physical mechanics the oxygen consumption should decrease. That this does not happen suggests that the larvae are somehow adapted to the range of pressures tested. If *Tribolium* is not native to higher elevations, such a response requires the presence of some type of physiological pre-adaptation to the atmospheric phase of this habitat. One possible explanation for the observed phenomenon is that the oxygen carrying capacity of the tissue fluids is so great that even at 14,000 feet the cells still get an excess of oxygen. However, the greater slope of the temperature response curves at higher altitude suggests that work is being done somewhere in the adjustment to these altitudes. This may be manifestation of the type of physiological acceleration associated with altitude suggested by Bullock (1955).

These results raise problems concerned with physiological adjustments to temperature and atmospheric pressure as ecological agencies. They will be used as guides in a continuing investigation into the ecological phenomenon of high altitude of which this paper is a part.

SUMMARY

Rates of oxygen uptake were measured for 2 size-age classes of *Tribolium confusum* larvae under 9 different treatments of temperature and altitude. The larvae were exposed to 3 different temperatures of 10° C, 15° C, and 24° C in 9 possible combinations with 3 different altitudes: sea level (simulated), 6750 feet, and 14,000 feet (simulated).

1. In all combinations the small larvae showed a greater rate of oxygen uptake per unit weight.

2. In all combinations and in both classes of larvae a

rise in the rate of oxygen uptake paralleled a rise in temperature.

3. In all combinations and in both classes of larvae an apparent rise in the rate of oxygen uptake accompanied a rise in altitude (a lowering of atmospheric pressure).

While items 2 and 3 above show the same trend, the nature of the adjustment is apparently different. The adjustment to temperature seems to employ physiological processes in which the physical expansion of the atmosphere is relatively unimportant. On the other hand the apparent increase in the rate of oxygen uptake that accompanies lowered atmospheric pressure reflects the use of more widely spaced gas molecules. The ability of the larvae to maintain a relatively constant rate of oxygen uptake in spite of falling atmospheric pressure indicates the presence of a type of physiological preadaptation.

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MORTALITY OF THE GOLDENROD GALL FLY, *EUROSTA SOLIDAGINIS* IN THE VICINITY OF ITHACA, NEW YORK

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Research over a 3 year period (Uhler 1951) on the life history of the goldenrod gall fly, *Eurosta solidaginis* (Fitch) showed that it was possible to determine annual mortality by examining over-wintering galls. The present study is a summary of 14 consecutive years' data (Table I).

TABLE I. Fourteen years (1947-1960) cumulative data on survival, parasitism, and predation on *Eurosta solidaginis* (Fitch) in the vicinity of Ithaca, New York

Legend	Cumulative % survival	Annual range
Survival— <i>Eurosta solidaginis</i>	28.9	4.9-47.9
Parasitism— <i>Eurytoma obtusiventris</i>	30.0	18.8-56.5
Parasitism— <i>Eurytoma gigantea</i>	5.6	2.2-8.7
Predation— <i>Mordellistena unicolor</i>	10.0	2.4-37.4
Predation—Birds	2.3	0.0-9.3
Natural Mortality	23.2	15.4-35.5

During the study 17,198 galls were examined. These were collected at the rate of approximately 1200 galls annually from 4 widely separated areas in the vicinity of Ithaca, Tompkins County, New York. The collections took place during the last week of March and first week in April. Galls were gathered at random by walking through the areas, taking a gall every few steps. They were collected from goldenrods on the ground as well as those standing upright.

The parasites, predators and inquilines have been established and are reported numerous times in the literature (Brodie 1892, Fyles 1894, Harrington 1895, Ping 1915, Hughes 1934, Milne 1940, Uhler 1951, Judd 1953 and Miller 1959).

Milne (1940) estimated a reproductive potential of 75 eggs per female. My own studies indicate 200 plus eggs per female. This is sufficient to maintain the population in spite of the fluctuation in survival of the host insect from year to year (Figure 1). During the period of this

study no decrease in the number of galls in each locality was observed.

There are 2 parasites. The wasp, *Eurytoma obtusiventris* Gahan, is the principal one. The other, *Eurytoma gigantea* Walsh is reported by Miller (1959) to have 2 emergence periods annually; one in late summer, the other in spring. During the examination of several thousand galls, throughout the year, I have observed *E. gigantea* emerging only during June and July in this locality. I have never found any stage other than the larva in August. The previous year's gall, emergence hole included, often remains standing the following summer. Miller might have confused these with the current crop.

The beetle, *Mordellistena unicolor* Lec. is able to complete its development in the parenchyma of the gall. However, *M. unicolor* had broken into the central chamber of the gall and devoured the host larva or parasite, whichever was present, in 73.2% of the 2,292 galls in which it was found. Other than that of *M. unicolor* no predation or parasitism was observed on either *E. obtusiventris* or *E. gigantea*.

By examining the central cavity of the gall it is possible to tell which organism *M. unicolor* has preyed upon. If it was the gall maker (i.e. *E. solidaginis*) the fly larva will be absent and the cavity filled with fine sawdust. If *E. obtusiventris* has been the victim, the premature puparium of *E. solidaginis* is empty, the larva of *E. obtusiventris* having been eaten, and a clearly visible trail of sawdust extends through the chamber. If the victim was *E. gigantea*, the cavity is filled with the wasp's large black fecal pellets and the beetle's trail of sawdust. In a few instances *M. unicolor* was found in the central chamber with the living gall maker or one or the other wasp parasite. However, predation is the rule when it reaches this cavity.

The only bird seen feeding on the gall was *Dendrocopus pubescens* (Swainson), the downy woodpecker.

Under host survival (Table I) are listed galls containing the living larva or pupa. Since *E. obtusiventris* and *E. gigantea* are the primary cause of host death, all cases in which they appeared, whether living, dead, or eaten by *M. unicolor* are included. Predation by *M. unicolor* in-

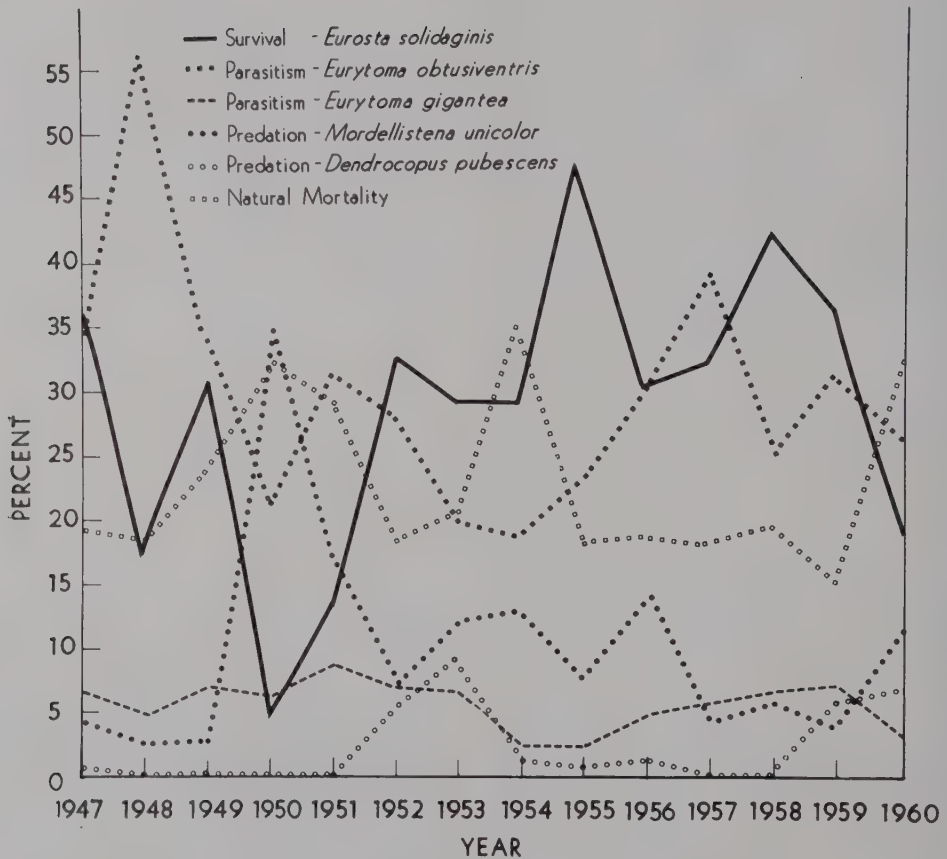


FIG. 1. Mortality of *E. solidaginis* in the vicinity of Ithaca, New York.

cludes only those instances in which the host insect was devoured. Under natural mortality are listed galls in which dead host larvae were present and all empty galls. Since the gall never forms unless a *Eurosta* larva invades the meristematic tissue of the goldenrod it is assumed that a larva had been present at one-time.

SUMMARY

Mortality data involving 14 consecutive years and the examination of 17,198 galls of *Eurosta solidaginis* (Fitch), the goldenrod gall fly in the vicinity of Ithaca, New York are presented.

The host, in spite of great fluctuation in survival from year to year, has maintained its numbers.

Data are given on parasitism by *E. obtusiventris* and *E. gigantea*. Predation by *M. unicolor* and birds are included. Under natural mortality are grouped empty galls and those containing dead host larvae.

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WINTER FISH MORTALITY IN PAMLICO SOUND, NORTH CAROLINA

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INTRODUCTION

Although mass mortalities of fishes from cold are well documented for coastal waters of Florida and Texas, they have not been reported for the sounds of eastern North Carolina. The occurrence of such a phenomenon in Pamlico Sound is recorded in this report, with observations on accompanying hydrographic and meteorological conditions.

OBSERVATIONS

During the first cold spell of the winter of 1958-1959, the appearance of great numbers of dead and dying fish on the southeast shore of Pamlico Sound was called to the authors' attention. On December 12, dead fish were observed at Buxton, where they had accumulated in a windrow that extended as far as one could see. Many other lifeless fish lay on the bottom in shallow water near the shore. Several days of cold weather had preceded this observation, and evidently the fish had died as a result of the cold. Water temperature was 41.4° F and air temperature, 36° F.

Only 2 species of fish appeared to be involved in this mortality: round herring, *Etrumeus sadina* (Mitchill), 5 to 7 inches long; and chub mackerel ("down-east mackerel" locally), *Pneumatophorus colias* Gmelin, 10 to 12 inches long. Round herring composed 99% of the dead fish, with chub mackerel forming only about 1%.

Later that day, similar windrows of dead fish were observed 8 miles west of Buxton, near Hatteras village, and at Hatteras Harbor, about 2 miles from Hatteras Inlet. The same 2 species of fish were involved along this part of the shoreline, with little change in their proportional representation. It was estimated that there were 35 dead fish to a linear foot of beach, leading to an estimate of about 2,000,000 herring and 20,000 dead mackerel on the shoreline from Buxton to Hatteras. While a few fish washed up on the shoreline north of Buxton, they did not appear in the great numbers that were observed west of Buxton. It was not possible to determine if the accumulation extended westward to Ocracoke Island, for high winds had curtailed ferry service to Ocracoke. The area in which dead fish were collected is indicated in Figure 1 by shading.

The fish bore no lesions, and it was assumed that they had been killed by cold. In Hatteras Harbor a number

were still alive and capable of fitful, ineffectual movements. They were apparently benumbed and relatively helpless, for waves would leave them stranded on the beach, unable to return to the water. While no chemical tests were made of the water, the presence of only these 2 species was taken as an indication that a toxic substance was not responsible for the mortality. The water was relatively clear and not clouded by suspended material. The accumulated fish were well preserved by the cold, and some were gathered by local fishermen who cooked and ate them without ill effects. Most were eaten by gulls, which soon gathered in large numbers. The coincidence of this mortality with the first cold spell of the season left little doubt that cold was the cause of death of these fish.

In seeking the cause of death, it was considered significant that the dead fish were not typical inhabitants of Pamlico Sound. Round herring were not recognized by the local sound fishermen, and our aid was sought for their identification. This species has only recently been reported from Chesapeake Bay (Massman 1960), and is rare in such inshore waters. Chub mackerel appear in small numbers in the catch of trawlers operating near Diamond Shoals Lightship. Since neither species is normally a resident of Pamlico Sound, it seems reasonable to assume that they were not already in the Sound, but were driven in by the severity of the northeast winds which prevailed for several days, and which were particularly strong on December 11, the day before the mortality. The known response of the waters of Pamlico Sound to winds lends support to the view that the fish entered through Oregon Inlet, rather than through Hatteras or Ocracoke Inlets.

Meteorological and hydrographic data

At Cape Hatteras the average air temperatures were above normal for November, 1958 (U. S. Weather Bureau 1958). During one 7-day period, November 23 through 29, the mean temperature was 5.9° F above normal. In contrast, December was 4.8° below the mean for a 30-year period, and northeasterly winds predominated.

In Pamlico Sound, wind tides exceed astronomical tides, except in the immediate vicinity of the inlets (Marshall 1951). Roelofs and Bumpus (1953) observed an instance of strong southwest winds producing a high wind tide in the northern part of the sound. By the same phenomenon, northeasterly winds could displace sound waters southwestward and produce a similar wind tide in the southern end of the sound. Under such conditions, the water level in the region of Oregon Inlet is correspondingly lowered and the incoming phase of the tidal cycle at the inlet is prolonged, the reverse of the situation described by Roelofs and Bumpus for southwest winds. In addition, northeast winds typically produce abnormally high tides on the other beach, which would reinforce inward water movements, and thus introduce a much larger volume of water to the sound through Oregon Inlet.

Ordinarily, water passing through Oregon Inlet does not seriously modify the north-south salinity gradient in Pamlico Sound; however, the much greater influx of ocean water under the influence of northeast winds does produce a wide-spread effect on the salinity pattern, shift-

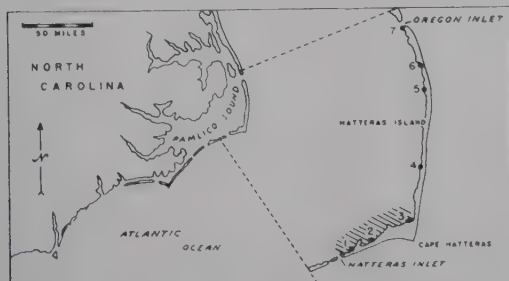


FIG. 1. Pamlico Sound, showing area of collection of dead fish, and location of hydrographic stations: 1—Hatteras ferry slip, 2—east of Hatteras village, 3—Buxton, 4—north of Avon, 5—Rodanthe, 6—"New Inlet," 7—Oregon Inlet.

ing the point of minimum salinity in the eastern part of the sound from Rodanthe to the Buxton region, 20 miles farther south. Figure 2 presents the salinity values obtained on December 2, 1958, after such a period of north-east winds. A set of values obtained without the influence of northeast winds is presented for comparison. From this increase in salinity, we can deduce that a large body of oceanic water also entered through Oregon Inlet during the period of high northeast winds that preceded the fish mortality.

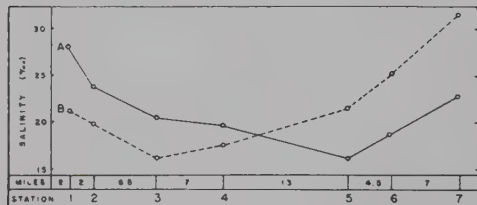


FIG. 2.—Salinity at hydrographic stations between Hatteras Inlet and Oregon Inlet: A—A, mean of observations made during 6 periods without northeast winds; B—B, observations for December 2, 1958, with northeast winds. Station 1—Hatteras ferry slip, 2—east of Hatteras village, 3—Buxton, 4—north of Avon, 5—Rodanthe, 6—“New Inlet,” 7—Oregon Inlet.

Weather conditions that preceded and accompanied this fish mortality have been analyzed with the aid of daily weather maps and local climatological data prepared by the U. S. Weather Bureau. Winds in the Hatteras area, which had been from the northeast since the 9th, rapidly increased in intensity with the approach of a low pressure system on the 11th (Figure 3). By 1 AM on the 12th, although it had become an intense storm with central air pressure of 29.18 inches, it was moving northeasterly, away from land. Winds in the Hatteras area shifted to north, then northwest, as the storm moved past. The counterclockwise circulation around this low pressure system helped draw cold polar air into the southeastern

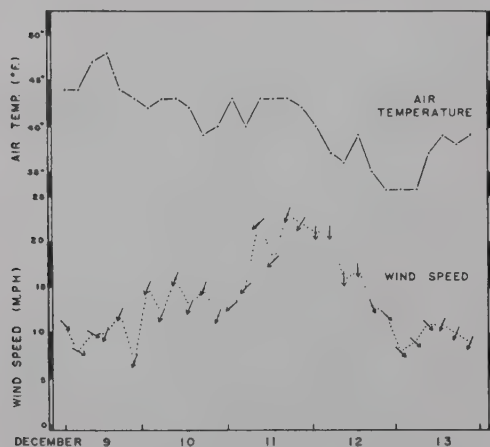


FIG. 3. Air temperatures and wind direction and force at Cape Hatteras, December 9-13, 1958. Data for 2, 6, and 10 AM; and 2, 6, and 10 PM, from U. S. Weather Bureau (1958).

states, carrying freezing weather to the coast as far south as Savannah, Georgia. The drop in air temperature that accompanied this shift in wind direction is plotted in Figure 3. The effects of these high winds and low temperatures can also be seen on hydrographic records for lightships off the east coast (Day 1960). At those stations, there is an interruption in the record on December 11 or 12 as the storm moved by, followed by significantly lower readings of surface temperatures. These low temperatures had a pronounced effect on the waters of Pamlico Sound, which, because of their shallowness, respond quickly to changes in air temperature. On this occasion the temperature of sound waters was reduced to levels not previously attained in the 1958-1959 winter season. Turbulence produced by the wind doubtless assisted in the loss of heat by the sound waters.

Once in Pamlico Sound, the fish were subjected to the rapid decline in temperature as these waters chilled. In their oceanic environment, these fish would not have been subjected to such sudden temperature changes. The rapid chilling apparently numbed them in such a way that their swimming movements were fitful and ineffectual. Incapacitated in this way, they were driven southward by wind-induced currents and wave action. Northwest winds helped concentrate them on the east-west shoreline of the sound from Buxton to Hatteras.

DISCUSSION

The shallow waters of Pamlico Sound make this body of water susceptible to rapid chilling in late fall. Roelofs and Bumpus (1953) state that the mean depth is probably not more than 15 feet; because of this shallowness and the almost incessant winds, there is almost no stratification. The effects of air temperature changes would be most marked in the broad shoal areas in the eastern part of the sound, bordering on Hatteras Island.

When northeast winds produce a greater than normal influx through Oregon Inlet, this water mass will most likely flow southward over these shoals on the inner side of Hatteras Island. By this combination of hydrographic factors, the parcel of oceanic water is quickly brought into a position where it is subject to maximum exchange with the atmosphere. When northeast winds coincide with or are immediately followed by a cold wave, this oceanic water is quickly chilled. Consequently, animals that cannot tolerate rapid cooling may be temporarily incapacitated or killed by the cold.

As noted by Winslow (1889), strong northeast winds produce a high wind tide in the southern part of Pamlico Sound. Higher water levels on the sound side of Hatteras and Ocracoke Inlets would prolong the out-flowing phase of the tidal cycle at these inlets and correspondingly shorten the in-flowing phase. Because the chub mackerel is at the southern edge of its range in the Hatteras area, this species would not have been engaged in an active southward migration at the time of the mortality, and there is no indication that the more abundant herring were, either. Presumably, the presence of the affected fish in Pamlico Sound was a consequence of water movement through Oregon Inlet on an unusually large scale.

This mortality evidently resulted from the coincidence of several apparently independent factors: (1) a delayed cooling of sound waters in the fall, (2) a prolonged period of strong northeasterly winds, (3) a movement of temperature-sensitive fish into Pamlico Sound, and (4) a precipitous drop in air temperatures. The probability of having all of these requirements fulfilled and synchronized seems very small. In this connection, it should be noted that local watermen could not recall a similar mass mortality in these sound waters. Evidently,

such large-scale winter fish mortalities are a rare occurrence in Pamlico Sound.

Storey and Gudger (1936) reviewed the occurrence of mass mortalities of fish caused by cold on the Gulf Coast of Florida, and Gunter (1945) discussed the occurrence of such mortalities on the Texas coast. In addition, the effects of a cold spell on fishes on the southeast Florida coast have been described by Miller (1940), and for Key West by Galloway (1941). Such mass mortalities are common in the shallow bays and lagoons of the Gulf Coast, occurring at least once every decade. They follow the same pattern, with the fish mortality coinciding with or following immediately after a cold wave.

Storey (1937), comparing the ranges of Florida fishes with their relative susceptibility to cold mortality, found that tropical species were more often killed by freezes at Sanibel Island, Florida, than were species with subtropical ranges. Fishes with a temperate range were least susceptible to cold. The round herring would be classified as a temperate-subtropical species, being distributed from the Gulf of Mexico to Cape Cod, with stragglers to Maine (Bigelow & Schroeder 1955), and the chub mackerel would be classified as a cold temperate species, being distributed from Cape Hatteras to the Gulf of St. Lawrence. Evidently, the species involved in this mortality do not show a clear correlation of latitudinal range with susceptibility. If a full list of species present in Pamlico Sound were available, it would probably show that the significant difference between the normal ranges of susceptible and surviving species lies in their habitat preference, *i.e.* whether they are primarily oceanic or are typical inhabitants of bays, sounds, and similar inshore bodies of water.

ACKNOWLEDGMENTS

These observations were made in the course of research supported by a grant (G-5838) from the National Science Foundation. The authors also wish to thank the Cape Hatteras National Seashore of the National Park Service for its aid and support; and Ben Williams of the Cape Hatteras Weather Bureau for critically reading the manuscript.

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ORDINATION OF THE PLANT COMMUNITIES OF WISCONSIN¹

In 1926, Gleason put forward his hypothesis of the "Individualistic concept of the plant association." Professor J. T. Curtis, Head of the Plant Ecology Laboratory of the University of Wisconsin, has accepted this hypothesis as a basis for the description and ecological analysis of the vegetation of Wisconsin. What has been achieved in little more than a decade is an outstanding tribute to Professor Curtis and his co-workers' industry, clarity of planning and ability to handle, present, and interpret many varied kinds of basic information concerning the vegetation, its history, relationship to environment and the autecology of individual species. It is not intended here to discuss the relative merits of Professor Curtis' methods and his views on the systematisation and the classification of ecological information. Rather it is the aim of the reviewer to assess this work as a contribution to plant ecology.

THE VEGETATION OF WISCONSIN is not a book cast to be of parochial significance. Curtis' breadth of approach, methods of investigation, and presentation of results and their interpretation are a major contribution to the development of plant ecology. The application and elaboration of his methods and concepts elsewhere should do much to advance ecological research.

Presentation is clear, and is enhanced by the author's avoidance of the use of technical terms (those which are used are fully explained either in the text or in a special glossary). This should make the book easily understood by those who are not specialists in plant ecology or are not familiar with the vegetation of North America.

The book is divided into seven parts, which deal with the general background to the studies (the flora, environment, distribution of plant communities, and methods of study); the southern and northern forests, savanna and scrub communities, certain lesser communities, and finally an important and stimulating consideration of the vegetation as a whole. A compact, but very informative appendix gives basic data concerning each vegetation type discussed. The information includes a series of small-scale maps, each showing the distribution of the examples of the plant community studied, and of its original extent prior to intensive European settlement; quantitative data concerning the prevalent species of the communities; environmental relationships (soil and climate in particular); stability; related communities; geographical distribution, locations of typical examples, and reference to relevant publications. This way of presenting ecological information should be of general applicability. There is an extensive and valuable bibliography which includes 595 references to both American and European literature.

The basis of the ecological analysis and interpretation lies in the concept of a "vegetational continuum"—a series of plant communities whose floristic composition gradually changes along an environmental or developmental gradient. "No discrete divisions, entities or other natural discontinuities are present." Curtis maintains that plant communities are not classifiable in a manner similar to

taxonomic systems in biology. No two stands (specific examples of a vegetational type) are of the same composition, and they have no method of self-duplication, since the communities are the result of the chance of history and migration, partial catastrophic destruction and the influence of a widely varying environment upon a complex and variable population of species, no two species having the same ecological amplitude and each in turn showing a varying ecotypic response to environment. For the purpose of study and discussion plant communities can, however, be arranged in orderly but very broadly categorised groups.

Within the limits of this review, the details of the several quantitative vegetational measures and indices used for analyses of the characteristics and relationships of plant communities cannot be entered into. In practice they are simple and rapid to use. No single quantity determined for each species within a community is adequate to reflect its complex structure and its developmental status; rather, use must be made of several dissimilar quantities. This Professor Curtis has done, but he has gone further, and this, to the reviewer, is his most stimulating contribution. Several quantitative criteria are integrated into single indices. Firstly, at the species level, the *importance value* of a species or its significance in a stand or community is the summation of its values for relative density, relative frequency and relative dominance. Secondly, at the community level, a *compositional index* has been developed (it is not defined in the glossary) which is the sum of the products of the importance and adaptational value of each species within the community. The latter value is a subjective or rank estimate, based on an intimate knowledge of the autecology and seral relationships of the species concerned. This detracts from the value of the compositional index, but with this reservation in mind, the index can be ecologically meaningful, and usefully summates as one quantity a range of quantitative and developmental attributes. The complex and variable nature of plant communities makes it difficult for the human mind to categorise them by any simple means. The development of a single index, which integrates the quantitative characteristic of a community and broad ecological relationships of its constituent species is a significant attempt to resolve this difficulty.

Assigning a quantitative measure of the degree of difference between communities is a similar difficulty. Curtis has adapted a simple *index of similarity*, which has enabled him to show the relationships between various plant communities in a three-dimensional manner which may be interpreted ecologically. These problems can also be tackled by multivariate analyses, but the computational difficulties would be considerable when applied to such a large territory and range of communities. Curtis' methods are essentially practical, and the computations involved should not daunt even the most non-mathematically inclined of ecologists. Extensive and effective use is made of graphical representation of community and environmental inter-relationships.

It is difficult within the limits of a review to give a balanced account of the range of subjects and problems discussed by the author. The geographical relationships and post-glacial history of the vegetation of Wisconsin are

¹ Curtis, John T. 1959. The vegetation of Wisconsin; an ordination of plant communities. University of Wisconsin Press, Madison. xi + 667 pp., 53 figs, 30 tables, 66 plates. \$7.50.

dealt with in Chapters 1, 2, 3 and 22. The comparative effects of Indian and European man on the vegetation are well discussed in Chapter 23. The main phase of European settlement occurred between 1830-1850, and the records of the early land surveyors have provided material for an unique account of the vegetation immediately prior to intense settlement. It has been possible therefore to include within the appendix a series of maps showing the original distribution of many of the broad categories of plant communities studied, together with their approximate areas.

The book is illustrated by a well chosen series of sixty-six photographs of the main vegetation types discussed. The details of vegetation are satisfactorily brought out, but one feels that the reproduction of the plates by the publishers could be improved; they have a certain pale-ness and lack of contrast.

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BOTANY OF THE QUATERNARY¹

Fifty botanists from 16 countries joined to present and discuss these 40 papers on Quaternary botany and to take part in 5 field trips, one of 4 days duration. This report is concerned only with the papers presented, there being a guide for the excursions written by Dr. Lüdi. Many of the papers are only abstracted for this publication. The language of the papers is almost equally divided between German and English, with 1 each in French and Italian. Attendance was from most of the northern and western European countries plus Poland and Hungary. The USSR was not represented although fortunately Gams gave a richly documented report on recent activities in Quaternary botany by Soviet scientists. The U. S. was well-represented. Interest in Quaternary botany is perhaps indicated by the numbers in attendance from the different countries. The numerical order was—Germany, Switzerland, Denmark, U. S., then England, Norway, Poland, and Holland.

One would conclude from the papers that Quaternary botany is a branch of palynology. Over a quarter of the papers were concerned with palynological interpretations of postglacial vegetation, and almost as many were on interglacial vegetation. Techniques and pollen identification accounted for some 6 papers, and studies on taxonomy, chorology or evolution of plants for about a fifth of the total.

It is thus in the general field of postglacial and interglacial history of vegetation as shown by ecological interpretations of the pollens preserved in stratified sediments that most of the interest lay. However, the ecologist will also find interesting data on the contemporary influence of man on forest vegetation in Poland in Dyakowska's paper, on the ecology of soils in Florschütz' paper on the pollen content of podsol A₂ horizons, and on climatic changes in the papers on forest histories.

Although woody vegetation is the main kind discussed, a modern tendency to include the entire plant community is very evident. The papers by Zoller, Welten, Lang, van Zeist, etc. on the postglacial and by Watts on an interglacial deposit discuss many herbs as part of the pollen record. Obviously the interpretation of a pollen diagram is an ecological problem, as Iversen and Faegri have emphasized, so the more species that can be drawn into the analysis the more searchingly and accurately the ecology can be estimated.

¹Lüdi, W., editor, 1958. Verhandlungen der vierten internationalen Tagung der Quärtarbotaniker in der Schweiz vom 6-16 August 1957. (symposium) Veröffentlichungen geobotanischen Institutes Rübel in Zürich, Heft 34, 176 pp. + table. Verlag Hans Huber, Bern. 16.50 SFr (\$4.00).

Those interested in only autecology, or even taxonomy, will still find much of interest in this volume. The history of *Papaver* sect. *Scapiflora* in Scotland where the section is now extinct (It occurs at present in the European high mountains, Scandinavia, and the Arctic.) is discussed by Conolly. *Carpinus* and *Menyanthes* evolution in Poland is treated by Jentys-Szaferowa. Cereals in neolithic Poland are discussed by Szafer, *Ficus carica* in northern Italian bronze age settlements by Villaret-von Rochow, and *Castanea sativa* in the Tessin by Zoller. The latter and van Zeist include a number of weeds in their diagrams.

There is rich material here on vegetation history. In general C¹⁴ dating is commonly used and, as Welten emphasizes, such absolute dates can be used to order even fragmentary pollen profiles into a general, regional scheme of vegetation history. Some noteworthy papers are the following: The deep core from the San Augustin Plain in New Mexico reaches back into the Pliocene. Climatic implications are discussed by Clisby, Foreman, and Sears. Deevey correlates many pollen sequences in eastern North America in a fine summary paper. Gams' concisely summarizes Soviet work since 1950 with 114 references. Leopold compares the percentage *Picea* pollen in present pollen rain with present abundance of *Picea* in the forests of eastern U. S., and then compares the *Picea* fraction of the Two Creeks interstadial and later Valders maximum with similar data from the present. She concludes that the temperature of Two Creeks time was some 3-5° C cooler than the present in New England, and that Valders cooling lowered the temperature only slightly, more closely to the ice. A Günz-Mindel interstadial lacustrine deposit from near Bergamo in northern Italy still contained many Arcto-Tertiary trees such as *Zelkova*, *Juglans*, *Pterocarya*, *Carya*, *Cedrus*, *Tsuga*, etc. A Mindel-Riss interglacial flora of some 100 species from Ireland gives Watts the opportunity to discuss the Atlantic climate of Ireland at that time, the plant communities existing, extinctions of species, and even sub-specific identifications. Besides 5 species now found only in Britain, 7 others have become extinct in Ireland. They include *Picea abies*, *Abies* sp., *Rhododendron ponticum*, *Azolla filiculoides*, *Eleocharis ovata*, and 2 species of *Erica*. Welten presents a transect of 12 pollen profiles across the Bernese Alps into the upper Rhone Valley. C¹⁴ dates correlate the profiles which show differing dates of migration arrival by various species and their variations in abundance on the climatically different north and south sides of the mountains as climate itself changed. Detailed pollen profiles are presented by van Zeist with C¹⁴ dates. Correlations with human history, plant mi-

gration, and climatic history are made. Zoller presents from the Tessin variations in present pollen rain, a trenched profile in very great detail, C^{14} dating, correlations with the known forest history north of the Alps, and evidence that both Juglans and Castanea are here anthropochores. The natural occurrence of Ostrya on the other hand is shown not only by its disjunct stations

north of the Alps near Innsbruck and in Carinthia but also by the occurrence of its pollen at pre-settlement levels.

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PLANT GEOGRAPHY OF THE EASTERN ALPS¹

From 3 July to 7 August the 11th International Phytogeographical Excursion was held in the Italian Alps from Como through the Dolomites to Cortina and to Carinthia, Vienna, Salzburg and the Tirol in Austria. The total number of participants numbered 69, plus the 27 members of the two organizing committees, from 15 European nations. Of western European countries only Sweden, Portugal and the Low Countries were not represented by participants, of the eastern European only those in the extreme southeast were missing. The U. S. was unrepresented as usual.

This volume is not a guide to the excursion. The Italian and Austrian committees produced these to the extent of 274 pages as publications of the University of Florence and in Aichinger's ANGEWANDTE PFLANZENSOZIOLOGIE. These guides were richly supplied with maps, photographs, notes on geology and history, notable plant species, floristic lists, and references. Lüdi's volume consists of a chronicle of the 5 weeks and 8 papers arising out of discussions during the excursion. Seven of the papers are in German, 1 each in English and Italian.

The excursion traveled by bus, by jeep, by teleferique, and by foot. Always it had as guides botanists who had specialized in the region at hand. The flora was always known in great detail, geology was described, climates recorded, human history explained—in short all the ingredients for ecological study were present for the participants to integrate in what we may be sure were various ways.

The papers printed in this volume enlarge and elucidate many of the special problems brought up during the excursion. Tosca and Casas de Puig describe a moss association on tuff north of Bergamo. Pitschmann and Reisigl, the authors of the beautiful new flora of the south side of the Alps from Lake Garda to Como, discuss the

distribution, ecology, and history of many endemic vascular plants of the region between the Lake of Lugano and the Adige River. Species distributions are mapped in detail. This is plant geography at its best. Coombe contributes some fascinating ecological notes on British plants observed growing under quite different conditions in the Alps. Fenaroli describes a new subspecies of *Carex sempervirens* Vill.

In two papers on soils Haber describes a fluorescence method of determining numbers of bacteria and their activity by the CO_2 evolved *in situ*, and Welten discusses the pollen analysis of a solonetz soil profile with several humus horizons. The presence of quite different kinds of vegetation on the site during soil development is shown by the pollen analysis. It is obvious that pedologists in general are missing an important new tool in neglecting pollen analysis as a means of deciphering the history of soil formation and genesis. But pollen analysts could also profit by using such quantitative means of studying soil genesis as Barshad outlines in the volume on CHEMISTRY OF THE SOIL (ed. by F. E. Bear, Reinhold, New York, 1955:1-52).

Two long papers are devoted to the steppes met with east of Vienna. Wendelberger summarizes the chrono-, homo-, and litho-sequences of soils and vegetation in the pannonian forest-steppe and steppe region of lower Austria and Hungary. Limestone rocks, sands, saline deposits, and loess are the soil parent materials concerned. Eurotia, Stipa, Festuca, Kochia, Artemisia, Astragalus, Oxytropis, *Populus tremula*, Prunus will be familiar names to those studying American steppes. Lavrenko from the rich and broad experience available to a Soviet plant geographer distinguishes the Thymus steppe of rocky outcrops near Vienna from the central Asiatic Artemisia steppe. The two are related, but the Thymus steppe is closely related to Mediterranean vegetation.

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¹ Lüdi, W., editor, 1959. Ergebnisse der internationalen pflanzengeographischen Exkursion durch die Ostalpen 1956. (symposium). Veröffentlichungen geobotanischen Institutes Rübel in Zürich, Heft 35. 143 pp. Verlag Hans Huber, Bern. 15 SFr (\$3.50).

ENVIRONMENTAL CONSERVATION¹

It is possible to distinguish three fairly definite sets-of-mind within the large crop of current books on conservation. The first of these is essentially an economic one, favored in the operations of governmental agencies and of

¹ Dasmann, Raymond F. 1959. Environmental conservation. John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. xii + 307 pp., 153 figs., 11 tables. \$6.50.

the occasional industrial organization which has developed a conservation conscience, in which the practical sense of careful management of renewable resources and the prudent husbandry of non-renewable ones is explained and advocated.

Second is an approach in which one or another brand of evangelism, emphasizing either "goodness" or legal rights as much as common sense, prevails. This essential-

ly emotional view is the one usually employed in elementary school education and by the more vocal factions which concern themselves with our resources. While many exponents of this "people-oriented" view are guilty of seriously distorting facts, their approach does seem to be the only one currently capable of developing widespread public support for conservation legislation.

The third point of view is the purely biological one in which a straightforward presentation of the ecological basis of the renewable resources is made. This last view, based on the simple belief that there is a good deal of sense in man's learning to live with his environment rather than in spite of it, is abundantly represented in the literature²—and even within the books and releases of the other two groups—but, until now, it has not been adequately presented in textbook form.

Raymond Dasmann's *ENVIRONMENTAL CONSERVATION* will undoubtedly find an eager market in the teaching of conservation at the college level, for it is, above all else, good solid ecology. The book is intended for a one-semester course in conservation, presumably for students with some biological background and among whom there is considerable interest in the teaching profession, but could be used, with some supplementary reading, as a beginning text in ecology. Its distinctly western flavor may be a handicap for students in other areas, but since some of the best examples of both management and mismanagement are found in that region, this emphasis serves as an advantage as much as a fault.

The introduction to the book provides a clear expression of the theme—clear because this section is largely one of definition and thematic because it immediately establishes the point that renewable resources are integral parts of a larger, dynamically balanced environmental system. The major natural community types are then described, and the relation of human history to each of these is elaborated. Separate chapters follow on the most important individual resources, each presented in a way which assures the reader of a simple but accurate picture

of the ecological basis of the resource and keeps him reminded that no resource can exist or be managed without consideration for all of the others. Examples are neatly woven into all of the chapters so that organization and continuity of ideas are well maintained, and lively discussions of the controversies which are so much a part of conservation serve to add both meat and spice to the text. As an outspoken follower of Aldo Leopold, Dasmann is never one to stand on the middle ground (usually non-existent anyway) of such controversies, but he is always careful to describe the situation within which the other side lives and reasons. The chapters on range management and wildlife conservation (his own field) are especially good in this respect.

With so much effective presentation in the central chapters it is not surprising that the intended climactic chapter on conservation of environments appears flat. The idea that it is the whole environment of man with which we should be most seriously concerned rather than the separate resources has long since been accepted by any reader who has gotten as far as Chapter Ten, so there is little that can be said to interest him further at this point. Chapters on human population and the general outlook seem appended almost out of duty rather than integrated into the theme of the book. Perhaps future editions can be reorganized to strengthen this culminating portion of the book, but for the present, such strengthening scarcely seems to be needed, so convincing is all that goes before.

In playing down the dollars-and-cents approach and in keeping a firm check on conclusions which must stand on faith (or emotion) alone, Dasmann has accomplished the aims of the other two classes of conservation writer even more ably than they sometimes do themselves. Under his treatment, the economic sense and the "goodness" of conservation both become abundantly clear. The book is certain to receive heavy classroom use, and rightly so.

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² N. b. Graham's *Natural Principles of Land Use*.

THE BIOLOGY OF MARINE DETERIORATION¹

As Dr. Dixy Lee Ray states in the preface, "Even casual association with the sea serves to illustrate the extensive damage caused by marine animals that burrow in the piles, floats, wooden drydocks, and boats, and the deleterious effects of other organisms such as barnacles that foul ships' hulls." This volume includes the papers which were presented at a symposium held at the Friday Harbor Laboratories of the University of Washington. The symposium was sponsored by the University of Washington and the Office of Naval Research.

Throughout the book the biological aspects of the organisms which cause deterioration of manmade structures in the sea are emphasized. The biological context ranges from purely taxonomic contributions through the ecological factors which influence the attachment, growth and survival of the organism to purely laboratory studies

of the enzymatic activity of cell-free extracts. Nor do the authors let the word "marine" in the title limit their field of interest since in the section on cellulases they include discussion not only of the enzymes extracted from *Limnoria* and *Teredo* but range well onto dry land with a discussion of termite cellulase and cellulose digestion in insects. With such a broad scope of subject matter the reader should not expect an introductory or comprehensive discussion of marine boring and fouling organisms. The book is clearly written by the experts for the experts and those uninitiated in the art and science of marine boring and fouling organisms would do well to lay a good foundation before reading this volume. For those with adequate backgrounds new results and new approaches to the problems will be found.

The volume is divided into five main sections with thirty-four technical papers plus introductory statements to the volume as a whole and to each section. The first three sections are concerned with specific groups of marine organisms, and each starts with a taxonomic paper and

¹ Ray, Dixy Lee (editor) 1959. Marine boring and fouling organisms. (symposium) University of Washington Press, Seattle, Wash. xii + 536 pp., figs. & tables. \$8.50.

proceeds to discussions of the ecology and physiology of the organisms involved. These sections are Limmoria (7 papers), Tereidiniens (4 papers), Barnacles (4 papers), Cellulases (11 papers) and Economic Implications and Evaluation (8 papers).

The diversity in subject matter is nearly matched by the diversity of treatment which the various authors have given to their subject. The papers range from quite general, almost historical, reviews of work accomplished over the last decade or two to quite technical reports of work which appears to be the immediate research program of the author. For the uninitiated the reviews are not complete enough to help the reader put the more technical papers in their proper perspective. As one example of this: the discussion of fouling organisms is limited to the barnacles, and the only comment which indicates that these are not the only fouling organisms in the sea is found in the introduction to the section where Waldo Schmitt states, "some two thousand other species of marine organisms have been recorded as associated with barnacles and in their turn may initiate, or compound, barnacle fouling problems."

It may be surprising to the reader to find such a long section on cellulases, and to find discussed at considerable length many species which are foreign to the sea. As C. B. van Niel states in the introduction, if the discussion had been limited to the cellulases of the Tereidiniens and Limmoria it would have been very brief indeed. The similarity of the problem and the lack of agreement in studies of both the marine *Teredo* and the terrestrial termite make it clear that mutual discussion of the two problems may well produce new approaches to each. For both groups there are advocates of cellu-

lase production by the organism itself and advocates of the production of cellulase by associated protozoa, molds or bacteria. As is clear from reading this section, only further intensive work will solve some of the remaining problems. Certainly among the best of the studies reported in this section on cellulase activity is Dr. Ray's own paper on the cellulase from Limmoria. This is all the more noteworthy since it requires the dissection of the midgut tissue from approximately 600 Limmoria to produce one milliliter of crude homogenate.

In the section on Economic Implications and Evaluation the range of subject matter is again wide. It includes consideration of the nutritional conditions on the mineral composition of the wood and extends to evaluation of the use of specific preventatives such as sodium arsenite and coal tar creosote as effective inhibitors of marine deterioration.

The reader is left with the impression that this was a stimulating symposium for the participants. As Dr. Ray states in the preface, "For those who attended the Conference, further investigations have already been stimulated; for the wider audience that can now be reached, these pages may convey something of the freshness and enthusiasm that characterized the many thought-provoking discussions." This objective I am sure the book will achieve. The reader should approach it, however, in the attitude with which one approaches an issue of a scientific journal, and not expect to find a complete and broad discussion of the subjects in the title.

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POLLUTED WATERS¹

There is little that is new in Dr. Hynes' presentation, either in factual material or in point of view. Yet he performs a very useful task in gathering together a wide selection of information on pollution, obtained from his own research and from the pollution literature of the world. For this he is to be commended highly. It is felt, however, that he will appeal to a rather limited audience, and perhaps this was his aim. He will be far too technical for the average fisherman or industrialist, as well as for a sizeable proportion of the chemists, engineers and members of River Boards towards whom he professes to direct the book, for he is very profuse in his use of generic and specific names and of technical limnological terms. In order to aid the non-biologist to thread his way through the book, Dr. Hynes at the beginning devotes considerable space to a description of "natural waters" and of the biota of normal streams. In this section there are a number of illustrations depicting the organisms he discusses. Most of these are adequate for the purpose, although it is doubtful that the non-biologist will find them of great value in attempting to identify many of the organisms he may collect.

Dr. Hynes apparently has two main purposes in writing the book: 1) to summarize existing information for the benefit of those biologists and non-biologists who are

directly or indirectly concerned with pollution, and 2) to convince the English River Boards that they should hire biologists as consultants, inasmuch as pollution is primarily a biological problem, and not primarily chemical as the River Boards seem to think. Both of these aims are highly praiseworthy.

It is emphasized that except where pollution is severe the effects of dirtying the water do not differ basically from the processes that take place anyway in natural waters, albeit they occur naturally at a slower pace. Mild organic pollution results in eutrophication, but natural waters also become eutrophic from causes that are not man-made. Heavier pollution causes de-oxygenation of the water, sedimentation of decaying organic matter, and the growth of a collection of fungi, bacteria, algae and protozoans known to those concerned as "sewage fungus." But the same thing happens in natural waters where there is a heavy fall of leaves into the water. Even severe effects can result from natural causes at times.

By this reasoning the author is led correctly to the consideration that moderate pollution is not necessarily a bad thing, and that at any rate in any industrial society it is unavoidable. From here he concludes that the several conflicting interests involved in the use of natural waters can be reconciled, or at least compromised, and he proposes that in England the River Boards can act as impartial arbitrators: "This . . . is the duty of the River

¹Hynes, H. B. N., 1960. The biology of polluted waters. Liverpool University Press, Liverpool. xiv + 202 pp., 22 Figs., 11 tables. 25 s., \$3.50.

Boards, and there is little doubt that in time they will be able to discharge it effectively. Each will have to decide just what can and just what can not be allowed to enter its river at various points along its course, in order that a proper balance may be maintained between the various interests involved. Clearly, the standards will vary from place to place . . ." (pg. 168), and "This arrangement allows . . . flexibility; for instance, standards can be suited to local conditions . . ." (pg. 6).

In this approach Dr. Hynes shares a blindness with most recent conservationists in that he does not allow himself to recognize that there are such things as *irreconcilable* interests, and that government-appointed bodies such as River Boards seldom or never are really impartial because they are composed of humans who themselves take sides (as do conservationists also) according to their political and economic interests and their upbringing. Conservative County Councils and a Conservative Minister of Agriculture and Fisheries will appoint Conservative River Board members, and a Labor government will appoint those who have the presently dominating viewpoint of the Labor Party, and so on. In so far as a Board can be considered relatively impartial through the inadvertencies of its composition, the various conflicting interests will attempt to influence its deliberations by whatever means are available; and statistically it is the most powerful of these interests that will be served best, because it is best able to make itself heard.

In his final chapter ("The Prospects for the Future"),

Dr. Hynes goes beyond his River Boards and contemplates some partial solutions of the problems of damage and waste by pollution. But his schemes for the most part would involve organization on a far wider scale than that provided by local Boards responsible only for individual rivers, and thus would necessitate intervention on a national scale. National control by suitable governing bodies, however, requires that these governing bodies be responsive to the needs of the relatively un-vocal and unorganized multitude, rather than to the demands of a wealthy, powerful and aggressive minority. Presumably this would not be a line of thought that Dr. Hynes would willingly follow, or he would not decry in his concluding paragraph: "Recrimination and litigation may sometimes seem to produce rapid results, but they do not lead to good feeling nor to collaboration between the various interests concerned with inland waters" (pg. 175). Rather, he would draw the obvious conclusions (which he does not) from his previous statement: "New development schemes must take effluent disposal into account . . . There are hopeful signs that industry is becoming conscious of this point, *largely because of a number of prosecutions*, [italics mine—CCD] but it still often seems to be ignored by Government circles" (pg. 169).

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LIMNOLOGY OF LAKE OHRID¹

Lakes Tanganyika in Africa, Baikal in Siberia, and Ohrid, lying on the border between Yugoslavia and Albania, are especially interesting to limnologists and biologists because of their large proportion of endemic species. It is a pleasure to read a summary of existing knowledge of one of these lakes, written authoritatively by a man who himself played a key role in gathering the pertinent data. Prof. Stanković has a thorough knowledge of the widely scattered literature dealing with Lake Ohrid (his extensive bibliography contains references to papers written in nine European languages), and in addition he is aware of papers still unpublished, and of unpublished theses, for he has been intimately associated with the Hydrobiological Station in Ohrid, both as investigator and as director.

Beyond simply giving a summary of what is known scientifically concerning Lake Ohrid, Prof. Stanković takes every opportunity to point out the deficiencies in present knowledge, for there is very much that is insufficiently known, or entirely unknown. It is evident that he seeks to stimulate further study of the lake, and in this he is eminently successful. Each reader, as he covers the areas in which he has special interests, will see where further work needs to be done, whether he be a chemist, physicist, geologist, or biologist. If the reader, stimulated by the author, does not immediately pack his valise and head for Ohrid, then at any rate he dreams a bit. From among the dreamers eventually some will find a way to make their dreams come true.

The book's main emphasis is on the remarkable endemism of the fauna and flora, in so far as this has been studied. Thirteen diatoms have been described elsewhere only as fossils, yet they live today in Ohrid. Two of the three sponge species occur only there, as do many of the numerous turbellarian species. Ninety per cent of the 38 gastropod species are endemic, as are two-thirds of the 36 ostracods. Of 17 species of fish, 10 are endemic. In nearly every taxonomic group some of the forms are confined to Ohrid, or they have only a limited distribution elsewhere. Of the latter there are some, such as *Lamprodrilus pygmaeus*, occurring both in Baikal and in Ohrid, but no place else.

The wealth of endemic species is associated with two things: 1) the great age of Ohrid, dating from the upper Pliocene, and 2) its ecological isolation, lying in a karstic depression with a very small drainage area. The history of the lake has been one of great stability over long periods.

Lake Ohrid's ecology has been studied little, for most investigators have been concerned with faunistics. Prof. Stanković attempts to synthesize known ecological features, but he is greatly hampered by the unavailability of information. The lake is 286 m deep, and oligotrophic. Its waters are so transparent that diatoms grow even to a depth of 80 m. The author defines the littoral zone as that affected by wave action, hence down to 18-20 m. All of the macrophytes exist in this zone, but by no means all of the littoral is populated by macrophytes. The sublittoral is well marked, lying between 20 m and 40 or 50 m. Plants consist mainly of diatoms, but these are ecologically unimportant. The bottom is covered with fine sand and mud, with much organic matter,

¹ Stanković, Siniša, 1960. The Balkan Lake Ohrid and its living world. Monographiae Biologicae, Vol. X. Uitgeverij Dr. W. Junk, Den Haag. 357 pp., 101 figs., 33 tables. F 35.—

but its outstanding feature is a true thanatocoenosis of myriads of empty mollusc shells. The profundal is very monotonous, being lightless, of uniform temperature, and covered with an unvarying deposit of fine mud. An endemic species of blue-green alga, of unknown nutrition, occurs throughout the profundal, and nowhere else. The profundal fauna includes 1) eurybathic species, 2) relicts, 3) cavernicolous forms, and 4) autochthonous forms, the results of intralacustrine evolution. Oligochaetes, many of them endemic, are most characteristic, and profundal chironomids are almost lacking.

Despite its readability and its great usefulness, the book in places is rather repetitious. One wonders if a different organization of the material might not have eliminated this. For example, the first chapter deals with the geography and geology of the Dinaric region, and Chapter 2 deals with the morphology of Ohrid's basin and its hydrography. Then in Chapter 5 (Biogeography), in order to explain the peculiar nature of the endemic fauna and flora in terms of the history of the lake and its ancient character, the author deals again with the geologic origin of the lake, as well as of other Dinaric lakes. New geological information is given in this chapter, but for the reader to understand the new, he must be guided back through much of the old material again.

Also, within Chapter 5 itself, the author attempts to handle three closely related subjects separately. First he gives taxonomic lists of organisms known to occur in the lake, and discusses them in relation to their en-

demism. Then, after devoting many pages to a discussion of the history of the lake, he comes back to a biogeographical analysis of the biota. In this he is forced to re-discuss endemism, thus repeating much of the previous material. Thirdly he discusses the origin and history of the biota, and this requires still more repetition of both geological and biological information. Evidently Prof. Stanković wanted a section that would appeal to taxonomists, and he wanted also to appeal to geologists, ecologists and biogeographers whose primary interests are not strictly taxonomic. The book has suffered somewhat from this dichotomy.

Stanković, judging by the list of his publications in the bibliography, is more at home with French and German than with English. Nevertheless, his English is clear and unambiguous. Greater fluency perhaps might have allowed him to detect more of the typographical errors that occur especially in some of the later sections of the book, but few of these are a hindrance in understanding and enjoying the material at hand. Prof. Stanković is to be congratulated for his valuable and needed contribution. It is hoped that his success will stimulate active workers at Lake Baikal and Lake Tanganyika to produce similar up to date summaries of scientific studies of their own lakes.

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PRACTICAL ANIMAL ECOLOGY¹

Teachers of plant ecology have, for many years, enjoyed the benefits of several well-constructed texts and manuals devoted to field and laboratory techniques. Animal ecologists have, on the other hand, produced almost nothing comparable since Shelford's *LABORATORY AND FIELD ECOLOGY*, published in 1929. This may be partly due to the fact that plants are less inclined to wander about "at random," confounding attempts at orderly classification and study, yet excellent field and laboratory courses in animal ecology are being taught and many would undoubtedly lend themselves to textbook treatment.

This book is an outgrowth of such a course, given by the senior biology master of Winchester College. It is also intended as a supplement to his earlier text, *ANIMAL ECOLOGY*. The author bases the practical study of ecology on identification of animals and plants, life cycles and behavior, the influence of ecological factors, and numerical aspects of population relationships. An introductory chapter gives a very brief description of fundamental features such as food chains and ecological niches which are shared by diverse communities and habitats. This is followed by chapters on the measurement of climatic factors in air and water; collecting and marking methods; two chapters on qualitative studies and methods; and a chapter on the measurement of edaphic factors. Most of the remainder of the book is devoted to methods for the classification and study of particular habitats and com-

munities. The concluding chapter discusses organization of classwork and the evaluation and presentation of results. The appendices include a summary of W. B. Yapp's theory of line transects; a summary of the capture-recapture method developed by R. A. Fisher, and later summarized by E. B. Ford; and a guide to practical field study in the form of notes on the ecology of a chalk stream.

There is no question that a book of this sort would be useful in the teaching of animal ecology, but it is difficult to recommend this book to ecology teachers in North America. It is designed for students in school sixth forms (roughly equivalent to twelfth grade in the United States and Canada) and first year university and assumes an elementary knowledge of comparative anatomy and physiology. It is, therefore, unsuitable for high school teaching but could conceivably be adapted to college courses, if the treatment were not so provincial and the intellectual level of the book were more consistent. The author has used methods and examples which he is intimately familiar with, but has made no effort to survey the literature for other methods which may, in fact, be better and more generally used. Many of the methods and home-made apparatus that are described are unnecessarily crude and all too little use is made of general references that would allow the book to be adapted to teaching outside England.

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¹Dowdswell, W. H. 1959. *Practical animal ecology*. Methuen & Co., Ltd., London. 316 pp., 86 figs., 21 tables, 12 plates. 32s 6d.

A POPULATION OF LIZARDS¹

This well-written book summarizes 5 years of research near Austin, Texas, involving observations of over 3000 marked lizards (*Sceloporus olivaceus*). It represents a prodigious amount of field work by the author and at least seven graduate assistants. Never before has so much information pertaining to the natural history and ecology of one reptilian population been assembled, and the amount of raw data must have been immense. Following such a project it is a temptation to impress upon the reader just how much information has been gathered. But herein lies one of the merits of this book—Dr. Blair has done a good job of condensing and interpreting the data.

However, there is some question in my mind as to the pertinence of much of the material in Part III (Adaptation at the Individual Level). In a population study I do not expect to find 12 pages of text and figures devoted to the Tail, including breakdowns of tail breakage by age and sex and according to which quarter of the tail in which a break occurs. Similarly there is information on molts, scales, and claws (including relative lengths of toes), which seems more appropriate to a handbook of lizards than a population study.

The methods adopted (Part I) were routine, except for particular care in the registration and marking of newly born lizards. Thus a major problem in past studies of *Sceloporus*, viz. the accurate enumeration of juveniles, has been largely circumvented.

A discussion of environment (Part II) makes up about a tenth of the book. The main point is that 1954 was an exceptionally dry year. This emerges as such a significant fact in considering demographic changes between 1953 and 1956 that, were it not for the fact that any 5-year period in Texas is almost certain to include some sort of climatic aberration, one would conclude that Dr. Blair was fortunate in the timing of his study.

Part V includes a brief discussion of sex ratio (1:1 at birth) and convincing indications that males have a lower survival rate than females. There is also a wealth of quantitative data on the spatial organization of the population. Table 29, which gives 64 home ranges of different lizards (and of the same lizard at different ages), is particularly impressive. In Table 29 these areas are expressed in acres (e.g. .084 acres), a measure which I find difficult to visualize. In Table 27 and in the text another measure is used which I find more easily conceived—the square root of the area in square feet. It is shown that adults have larger home ranges than juveniles and that males have larger home ranges than females. An interesting sidelight is that, although adult females have home ranges averaging around 3000 sq ft, they usually make an egg-laying excursion beyond the limits of their home range, often ignoring perfectly suitable sites within their normal domain. There is a comprehensive discussion of dispersal of young lizards with 6 figures illustrating the movements and eventual relocation of over 160 juveniles.

Part IV constitutes a singular achievement in the field of population ecology, not only as a detailed recapitulation of 5 years of demographic change, but also as a con-

tribution towards understanding the natural regulation of numbers. The size and age-composition of the population was determined for each of 5 consecutive years, and from this information (coupled with reasonable assumptions as to age-specific fertility) the total reproductive potential estimated.

Some difficulties were encountered in accounting for the fate of the estimated reproductive effort. Wholesale destruction of nests clearly accounts for the greatest losses, but because the fate of only about one-fourth of the potential number of nests was definitely known there is uncertainty as to the amount of loss between egg and hatching. One factor which must have had some influence in the course of this study was the artificial protection of nests. The efficiency of the patch-nosed snake (*Salvadora lineata*) in locating nests and eating eggs is such that, had nests not been protected by wooden frames, nest destruction would have been appreciably greater.

Blair estimates the hatching by two methods, both admittedly approximations. One method, depending on the assumption that all hatching broods were registered, seems unsound and was actually rejected by the author because it predicted fewer young than were actually captured and marked in 1955. The other method is a proportional technique which yielded more credible estimates and seems theoretically superior. This method could have been strengthened had a method of estimating variances been devised. Because the proportional method seems more reliable than the so-called "broods" method, I think there are strong indications that the hatching success indicated for 1955 in Table 21 is too low, and the statement on p. 99 confusing in the light of estimates developed by the proportional method.

The survival of hatchlings is taken as the difference between the estimated hatch and the number of young-of-the-year registered. Here there is an unexplained inconsistency between Table 25 and Table 26. The survival of 1952 hatchlings is given as 94 in Table 25; in Table 26 the 1952 survivors total 93. Similarly Table 25 indicates survival of 115 hatchlings in 1953; Table 26 gives the 1954 recruitment as 105.

However, the main point developed is that whereas the survival of young in 1952, 1953, and 1954 is on the order of 2.7% (of total estimated potential), the survival in 1955 (following the heavy adult losses of 1954) is about 5.6%. So it is relatively immaterial how the mortality between egg and maturity is distributed. If we accept the estimates of potential production (which seem carefully drawn), then the survival of young (as determined by the thorough census procedures characteristic of the study) was about twice as good in 1955 as in the previous 3 years. Furthermore, the absolute number of lizards surviving to maturity varied only from 93 to 115 over 4 years, even though the reproductive potential ranged from 1957 to over 4000. As Blair points out, this is strong evidence in favor of density-dependent regulation of numbers. Other information presented indicates that the restriction is imposed by a fixed number of suitable shelters and not limited food supply. It would be interesting to observe the effect of the establishment of artificial shelters in an area of known carrying-capacity (Blair's 10 acres seem to support about 200 lizards).

The photographs in the book are good and the figures

¹ Blair, W. Frank. 1960. The Rusty Lizard; a population study. University of Texas Press, Austin, vi + 185 pp., 31 figs., 35 tables. \$4.50.

skillfully drafted (although the lettering is too heavy in a few). The cover is a nice example of apatetic coloration—it takes close scrutiny to find the lizard as well as part of the title and the author's name. Dr. Blair and his students have accomplished a major piece of work in this study. The necessity of several years of consecu-

tive observation is clearly indicated—such a project is not recommended until tenure has been obtained.

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RECENT PROGRESS IN COMPARATIVE ENDOCRINOLOGY¹

From May 25-29, 1958, Columbia University sponsored a symposium on Comparative Endocrinology that was held at Cold Spring Harbor. Most of the papers and a summary of pertinent discussion are included in this stimulating volume. Statistically, only about one-third of the papers are truly comparative, dealing with more than one major group; since "Comparative Endocrinology" seems to be defined as nonmammalian endocrinology by many of its practitioners this is not surprising. However, the papers dealing with single groups are organized around a comparative survey of a single endocrine function, which gives the entire volume a satisfying comparative flavor. With respect to papers that are largely restricted to single classes, some 6 deal primarily with fishes, 3 with amphibians, 5 with birds, 9 with mammals, 3 with invertebrates and only one exclusively with the reptiles. The dearth of information available on the reptiles is further demonstrated by the cursory treatment they receive in the chapters that consider several groups; the critical phylogenetic position of the Reptilia makes this neglect all the more unfortunate. After an introductory section containing some 5 generalized chapters, there is a section of 9 chapters on neuroendocrines and their interrelationships with targets and end points, 7 papers on the thyroid and related subjects, 6 on the pituitary, 8 on the gonad, 3 each on adrenal and pancreas and 2 papers on such equivocal structures as the urhypophysis and Staninus corpuscles. Although most of the papers attempt some review of their field, few are complete reviews that will give the casual reader a general synopsis and most deal with materials of current interest; the book is certainly not a classroom text.

A number of the papers will be of particular interest to ecologists. Hoar discusses the role of endocrines in ecological adaptations of fishes; he considers particularly seasonal changes, temperature tolerance, photoperiodic

responses, salinity tolerance, responses to dissolved gases, migratory behavior and habitat selection. Baggerman analyzes the effects of the gonad and thyroid on seasonal salinity preference in sticklebacks and salmon. Wolfson's review of photoperiodic and endocrine effects on spring migration in birds could be used as a starting point for future students. Christian summarizes the evidence for the exciting theory that endocrine responses to population density in mammals "... constitute a feedback mechanism which regulates the growth of mammalian populations." The possible contribution of endocrine dysfunction to density-dependent mortality and population growth factors remains to be assessed, but Christians' lucid discussion demands that ecologists working on vertebrate populations begin extensive analyses of the endocrine organs and their targets. For the behaviorist, Aronson considers phylogenetic aspects of hormonal control of reproductive behavior. Since the behaviorists were among the first ecologists to discover the interrelationships of ecology and endocrinology it is unfortunate that the behavioral effects of the endocrines were not more fully considered in this symposium. The remainder of the papers, while primarily directed toward endocrine problems, contain a wealth of information on the control of ecological responses in the major vertebrate groups, and a few invertebrate forms.

One final point—Dr. Gorbman is to be congratulated for the excellent job he has done in editing this volume. Unfortunately, however, the discussions from the floor have been edited to a point of literary sterility. Certainly the pertinent topics have been included, but the impertinent remarks, often so pregnant with new research ideas, have been lost to the editor's blue pencil. Dr. Gorbman's position must be appreciated, of course. The price of the book is already considerable and the addition of further, perhaps equivocal pages would certainly have added to cost. This book is highly recommended to the vertebrate ecologist who is interested in the physiological bases of the phenomena he observes.

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